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Studies on morphogenesis and development of the ascocarp of Sphaerotheca castagnei

ILLO HEIN

(WITH FIVE TEXT FIGURES AND PLATES 28, 29)

The structure of the ascocarp and the stages in its development have been fairly well understood since the time of De Bary, and the main points in his conclusions have been many times confirmed. The perithecial tissues are formed by aggregation of hyphae. De Bary characterized such structures as pseudoparenchymatous, and the term has been generally accepted. Little attempt has been made, however, at a morphogenetic analysis of the various growth factors, the hyphal contacts and pressures and the environmental stimuli by which the development of such structures is initiated and controlled.

LITERATURE

The literature concerning the morphology and development of the ascocarp of the mildews has been many times reviewed and analysed. I shall endeavor to summarize the data which relate to my own special problems under the following heads: (1) Pseudoparenchyma, morphogenesis, and tropistic responses; (2) Physiological species in the mildews; (3) Spore discharge; (4) Epiplasmic granules in the ascus.

Pseudoparenchyma, morphogenesis, and tropistic responses. The development of parenchyma-like tissue from filamentous hyphae was first studied by De Bary (1863, 1870) in *Erysiphe* and in *Eurotium* and by Woronin (1869–70) in *Sordaria*. De Bary described in some detail the formation of such pseudoparenchymatous tissue in the development of the perithecia of *Podosphaera tridactyla*, *Sphaerotheca castagnei* and in *Eurotium glaucum*. As is well known for ascomycetes generally the ascogonium becomes covered with an inner and an outer layer of parenchyma-like tissue which is formed by the growth, branching, and interweaving of hyphae. The hyphae divide only by transverse septa

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and ultimately fill in all inter-hyphal spaces, forming an unbroken tissue. Bauke (1876) distinguished three methods of pycnidial development to which Zopf (1881) gave the names, "Hyphenfrucht," "Gewebefrucht," and "Knäulfrucht." It has been claimed by De Bary (1884), von Tavel (1886), Schnegg (1915), and Kempton (1919), and others that the walls of certain pycnidia develop by division in three planes (meristogenetic) while others are formed symphyogenously by the interweaving of hyphae and hence consist of pseudoparenchyma. The "Hyphenfrucht" and "Gewebefrucht" of Bauke and Zopf are variations of De Bary's meristogenic types. Kempton (1919) concludes that the meristogenous method is the more common and is of two types, simple and compound, while the syphyogenous method is less often found.

Hoffman (1856), Hartig (1874), Göbel (1902), Fayod (1889), and many other later students have reported detailed studies of the morphology, growth, and development of the fleshy fungi but have taken little account of the morphogenetic factors involved.

From a study of *Agaricus campestris*, W. Magnus (1906) concludes that certain specific, organized parts of the pseudoparenchyma create growth inhibitions against the organism as a whole, so that certain tissues of the sporocarp give rise in regeneration to similar tissues only; for example, the hymenium can give rise only to hymenial tissue. The regeneration of a normally lamellate hymenium may result, however, in a decidedly toothed, tubular or netlike hymenium. This condition is not to be regarded as atavistic in the Weismann sense, even though such forms are according to present phylogenetic views lower, but is due to the mechanical conditions under which the regenerative growth takes place. Transformation of vegetative to reproductive tissue results in a loss of the capacity for regenerating the whole sporocarp. So long as the tissue is still vegetative it possesses in a high degree the capacity to regenerate itself, but at a certain stage it becomes reproductive and loses its capacity for regeneration. W. Magnus also holds that the exhaustion of foodstuffs in the substratum as well as the transition to aerial growth must be of importance in determining the initiation of sporocarp formation. That the transition to an aerial environment is insufficient, as W. Magnus notes, to cause sporocarp develop-

ment is shown by the fact that in dark, poorly ventilated cellars the mycelium may grow upon the surface of the substratum for days without producing sporocarps. Mere transition from growth below the substratum to aerial growth does not suffice to initiate the development of fruit. Similar conditions were observed under bell jars placed over cultures. The hyphae grew profusely under the bell jars without producing sporocarps, while immediately outside the jars numerous sporocarps developed. Light seems to be unnecessary for the development of *Agaricus campestris*, growth and differentiation going on equally well in darkness.

Atkinson (1906) recognizes certain factors in the development of the pileus of *Agaricus campestris* as follows: "The growth of the pileus which at first is strongly hyponastic becomes less so as the pileus expands. The upper surface gradually ceases to grow and the extension of the underlying part often tears the cuticle of the pileus into fibrous scales. The growth of the pileus gradually becomes epinastic, as the lower area and the hymenophore with the gills now grow more rapidly than the middle and upper portions. This causes the pileus to become plane, or in old specimens the margin itself becomes upturned." De Bary had already described the later growth stages of the pileus as epinastic.

The geotropic responses of the sporocarps, as they occur in nature, have long been known. Brefeld (1883), Buller (1909), and W. Magnus (1906) have reported important experimental results on the geotropic and heliotropic behavior of many species. Buller (1909) reports that the stipe is indifferent to geotropic stimuli before the pileus is developed, after which it becomes positively heliotropic and rectipetal in darkness. Buller states that the position of the gills is always very delicately adjusted by geotropic stimuli. The positively geotropic response is of great importance for successful spore liberation, since these are discharged by dropping downwards and easily lodge on the gill lamellae if the latter are not exactly vertical.

In petri dish cultures of *Lasiobolus pulcherrimus* Delitsch (1926) finds that the main hyphae of the mycelium grow radially from the spore, and the secondary directions of growth are thought to be determined largely by the tendency of the hyphae to enter areas unoccupied by other hyphae.

Physiological species in the mildews. Apparently P. Magnus (1898) first published the results of infection experiments with parasitic Erysiphaceae. P. Magnus reported the transfer of *Sphaerotheca castagnei* (Lev.) from the hop to *Taraxacum officinale* but his results were not confirmed by Neger (1902). Salmon (1904, 1907) found that *Sphaerotheca humuli* from *Potentilla reptans* would not infect *Agrimonia Eupatoria*, *Alchemilla arvensis*, *A. vulgaris*, *Fragaria*, *Poterium officinale*, or *Spirea ulmaria*, all of which are hosts for *Sphaerotheca*. *Sphaerotheca humuli* var. *fuliginea* from *Plantago lanceolata* would not infect *P. major* or *Taraxacum officinale;* and *Sphaerotheca humuli* var. *fuliginea* from *Taraxacum* would not infect *Fragaria*, *Plantago media*, or *P. lanceolata*, all of which are hosts of morphologically similar forms of *Sphaerotheca humuli*.

Steiner's (1908) results from experiments with *Sphaerotheca humuli* within one host genus, *Alchemilla*, led him to assume the existence of "kleine biologische Arten." Reed (1908) has summarized the literature of inoculation experiments with the mildews and states that in his opinion most of the results rest upon inadequate data. Woronichine (1914) failed to obtain infection on peach leaves with *Sphaerotheca pannosa* from the rose and failed also in the reciprocal experiment, though the forms on both plants are morphologically indistinguishable.

De Bary's morphological work on *Sphaerotheca castagnei* was done on material from *Taraxacum officinale*. Harper (1895) and Dangeard (1896) worked on material from the hop, and Winge (1911) worked on a *Sphaerotheca* from *Melampyrum* in Sweden. It would appear probable from the studies noted that there are many physiologically different races of *Sphaerotheca* as well as of other mildews, and Gäumann's work on other fungi suggests the possibility that there may be structural differences paralleling the physiological specificities.

Spore discharge. In *Sphaerotheca* and the other mildews spore discharge involves, first, the rupture of the cleistocarp and, second, the escape of the spores from the ascus. The rupture of the cleistocarp was first described for the Erysiphaceae by Wolff (1872), later by Smith (1884) for *Erysiphe graminis*, and by Salmon (1903) for *Sphaerotheca*. The mechanism of discharge from the ascus has been frequently reported on for the club-shaped asci and has been fully described by Buller (1909) for a

number of forms. De Bary states that in the Erysipheae spore discharge is simultaneous. Wolff (1877) finds that in *Erysiphe* the spores are liberated through a longitudinal slit in the apex of the ascus. Smith (1884) found that in *Erysiphe graminis* spores and sometimes asci are ejected forcibly from the ascocarp. Salmon (1907) describes the process as observed in *Erysiphe graminis*. The spores after the ascocarp has undergone a resting period are ejected forcibly into the air to a distance of 2 cm. from the ascocarp. According to Salmon the perithecium opens by a horizontal slit at one side somewhere about the equatorial plane. This slit gradually extends until the upper half is set free like a lid. Salmon states that the dehiscence is probably brought about by the swelling of the inner layer of the perithecial cells. In *Sphaerotheca* a vertical slit appears in the perithecium and the ascus protrudes from it, swelling to several times the diameter of the perithecium. The walls of the ascus become tense, the ascospores collect at the apex, and are finally discharged forcibly through a slit. Occasionally an ascus slips out of the perithecium, ultimately bursting to discharge the spores. Recently Ziegenspeck (1926) has given an adequate review of the literature and has made a detailed study of spore discharge of many different forms of Ascomycetes, but no data as to spore discharge in the Erysiphaceae are given.

Epiplasmic granules in the ascus. Most of the literature has been summarized by Guilliermond (1904) and by Pénau (1912). Zopf (1887) described disc-shaped granules and granules of variable shapes, generally six to eight microns in greatest diameter, in the conidia, conidiophores, and germ tubes of species of *Erysiphe*, *Podosphaera*, and *Sphaerotheca* which he believed to be reserve carbohydrates and called "Fibrosinkörper." Maire (1905) described metachromatic granules in Ascomycetes and Basidiomycetes and believed them to be not particular kinds of granules, but granules belonging to the vast class of Altmann's granules which are very variable chemically, depending on the species of plant in which they occur.

The granules described by Guilliermond (1904) in the epiplasm and the sporeplasm of *Aleuria cerea*, *Helvella sulcata*, *Ciboria uliginosa*, *Pustularia vesiculosa*, *Otidea onotica*, *Peziza venosa*, and other *Peziza* species stain bright red with Unna's polychrome blue after fixation with picroformol. Hemalum

gives clear differentiation of the granules with alcohol as a fixative, but is very poor when used with picroformol.

Meyer (1904) describes, in *Penicillium glaucum*, *Aspergillus glaucus*, and the Basidiomycetes, algae, gymnosperms, and angiosperms, granules, similar to those which he earlier described in bacteria and called volutin. In unstained living *Penicillium* and in *Aspergillus* the granules can be recognized only with difficulty but with methylene blue (1 to 10) they stain dark blue in color, darker than any other parts of the cell. With carbol fuchsin the granules stain a deep red color. Delafield's haematoxylin (10 drops in 5 cc. water) produces a dark blue color when the granules are treated with carbolic acid, but when Flemming's fixative is used pale-blue stained granules result. Fresh material, as well as material treated with formalin plus 3 per cent acetic acid, when stained with alcoholic or aqueous solution of ruthenium red gives red-brown colored granules. Meyer states that the granules are present in all parts, from the germinating conidium to the newly produced spore of the vegetative plant of *Penicillium glaucum*, but their occurrence in the ascus is not mentioned.

OBSERVATIONS

The development of a three or more layered pseudoparenchyma of cells progressively differentiated from the surface inward and enclosing a single large cell, the ascus, as we find it in *Sphaerotheca*, or a group of such cells as in *Erysiphe*, may be regarded as typical for all the powdery mildews.

The mycelium

The general facts as to spore germination and the nature of the mycelium are well known but may be reviewed briefly as an introduction to the problems involved in the formation of the pseudoparenchymatous perithecium. The conidia on germinating give rise, generally at somewhat equal distances and in a horizontal plane, to three or four hyphae which grow out at right angles to the ellipsoid spore. At first the growth is very irregular but later tends more to be radial from the spore as a center. The hyphae are at first thick and tend to be nodular. Later they become more evenly filamentous in form (text figure 1, *1* and *2*). The patches of mildew generally are circular in out-

line, and examination with the lens shows that the general direction of growth of the hyphae is radially from the center. The mycelium is profusely branched, septa occur fairly regularly, and the cells are from 40 to even 80 microns in length. The average length of the mycelial cells is about 55 microns, which is similar to the average given by Bezssonoff (1914) for the mycelial cells of *Sphaerotheca mors uvae*, which he states are 57.6 by 5.4 microns. Where the mycelial network is especially well developed, septa are frequently rather close together, so that some cells are but 10, 15 or 20 microns long. The first septum is often formed a short distance, one to three microns, from the spore (text figure 2, 3). The hypha stains pale blue with the triple stain and Allen-Bouin fixation, while the cytoplasm of the spore stains a darker blue.

The factors determining the distribution of the mycelium include (1) those concerned with the general radial distribution of

Fig. 1. *1* and *2*. Germinating conidia with characteristic irregular, gnarled germ-tubes and radially growing mycelium.

the hyphae about the spore; (2) those which determine their contact relations with the host surface; (3) those which determine the angles that the successive sets of branches make with each other.

As noted, the spore on germinating sends out from one (text figure 1, *1*) to three (text figures 1, 2 and 2, 3) germ tubes, some of which may be very stout, gnarled, irregularly shaped structures from which other similar irregular hyphal branches or the characteristic mycelium may arise (text figure 1, *1* and *2*). A hyphal complex is thus formed; and about this there is a somewhat radial orientation of the profusely branched hyphae. The branches may arise either slightly below the septum or nearly midway

between two septa. The problems as to the direction of growth and method of branching of the hyphae here are essentially similar to those involved in the distribution of roots and branches in the higher plants. Chemotropic stimuli depending on the distribution of the food supply may be significant in determining the distribution of the ultimate hyphal branches. Whether moisture in hygroscopic relations or contact in thigmotropic relations determine the close adhesion of the hyphae to the host leaf is not easy to determine. The appresoria from which the haustoria arise are adhesion organs, and it seems probable that in some degree their development is regulated by tactic stimuli.

A fact that tends to support the assumption of hygromorphoses on the part of the hyphae is the very frequently profuse growth of the fungus in the grooves formed along the juncture of veins and leaf lamina.

In field plants the mildew first makes its appearance on the under surface of the leaves, where because of shade, more numerous stomata, and thinner cuticle the vapor pressure in the thin film of atmosphere immediately surrounding the leaf is probably higher than on the upper surface. In green-houses, where the absence of strong air currents tends to permit greater vapor pressure on both leaf surfaces, and where the general atmosphere tends to be more moist, the difference in vapor pressure between upper and lower surfaces may be less important. On green-house plants the mildew generally appears first on the upper leaf surfaces, perhaps because more spores lodge there and, finding favorable conditions, germinate and grow in situ. Eventually in the green-house the mildew also appears on the under surface of the leaf. The whole complex of factors influencing infection probably favor the under side of the leaf in field plants and the upper side in green-house plants.

That the mycelial hyphae may be reciprocally negatively chemotropic is to be considered. From his observations on *Lasiobolus pulcherrimus* grown on solid media in petri dishes Delitsch (1926) holds that the growth form of the mycelium is due to the dominately radial growth in the main hyphae and to mutually repellant chemotropic influence between all hyphae. Müller (1922), from observations made on the *Saprolegniaceae*, also suggests negatively chemotactic response as causing hyphae to grow apart from one another.

After the infected area is older, the later formed hyphal branches grow in all directions, filling in unoccupied areas. The typical radial distribution may be based on morphaethesia in Nöll's (1900) sense—that is, "Empfindungsvermögen für Form und Lage des eigenen Körpers." The deviation from the typical will be the result of various morphotic responses in Pfeiffer's (1925) sense.

Development of the primary envelope (cortical layers of the perithecium)

The term *perithecium*, though loosely used to designate the entire fructification, asci, enclosing envelope, etc., is properly used to designate only the enclosing hyphal layers, whereas the whole fructification is the *ascocarp*. I shall distinguish the outer protective cell layers as the cortex to distinguish them from the inner nutritive zone.

While the data are fragmentary and the methods of morphogenetic analysis for the thallophytes are as yet very poorly developed, it would seem that with the mass of structural and morphological material already at hand a beginning in the attempt to recognize the form-determining stimuli in the case of the ascocarp should be made. The work of W. Magnus (1906) and of Buller (1905) on the carpophore of the Basidiomycetes is suggestive of what can and should be done for the Ascomycetes.

The ascocarp begins its development after fertilization has been accomplished. There can be no question that the ascocarp is, however, strictly gametophytic in its origin. Brefeld's (1883) and Dangeard's (1896) contention that the sex cells are not functional has failed of confirmation so far, but in any case there is no doubt as to the relations of the gametophyte and sporophyte in the makeup of the ascocarp.

The enveloping hyphae arise just below the septum which cuts off the oogone from the basal cell and at a corresponding level from the basal cell of the antherid. These enveloping hyphae closely follow the contour and direction of growth of the ascogone rather than that of the antheridial stalk cell. The stalk cell of the latter forms one of the series of enveloping elements. This discriminitive relation in the behavior of the enveloping hyphae with reference to the sex elements becomes

more and more emphasized as the primary layer develops. Harper (1905) shows that the antheridial cell in *Phyllactinia* becomes embedded in the layers of the perithecium, where it ultimately gelatinizes and degenerates. In the *Sphaerotheca* here described, the antherid and its stalk cell become a permanent part of the primary envelope, in which they may be readily distinguished from the hyphal cells (figure 19). In late stages the antherid and the stalk cell cannot be identified with certainty. In all probability these cells have expanded laterally during the distention phase of the perithecium and have come to resemble closely the other cells. The special relations of the enveloping hyphae to the oogone suggest the existence of chemical stimuli with close adhesion phenomena due perhaps to thigmatropism.

All the vegetative cells of the ascocarp manifest a strong tendency to become closely appressed to one another and to the sex cells, as is shown in both early and late stages by the flattening of their surfaces of contact. The tendency of the tips of the hyphae to be pointed with the apex drawn inward toward the surface of contact (figures 7, 12 and 13) is conspicuous and significant of the physical effects of close adhesion. That the tapered form of the tips of the young hyphae of the first enveloping layer is due to adhesion with the ascogone is obvious, since the apices of other hyphae that are quite free of any contacts are well rounded, tending to a least surface configuration. The total absence of inter-hyphal spaces and general appearance of compactness of the young ascocarp are also to be noted.

The vegetative hyphae in their upward growth tend to form a uniform palisade clinging to the oogone until they meet at the apex. Since generally they do not all begin growth simultaneously, but are formed in irregular succession and are of varying ultimate heights, the final arrangement at the apex generally shows little regularity. As noted, the basal cell of the antherid contributes enveloping hyphae as well as the basal cell of the oogone and in my preparations generally, and perhaps always, produces two hyphae in addition to the antheridial branch. Text figure 2, *4*, shows a characteristic view of the enveloping hyphae that arise from the antheridial basal cell. The cell farthest to the left (text figure 2, *4a*) represents the antheridial stalk cell, the apical part of which, with the antherid, is shown in text figure 2, *5a*. The middle, somewhat shorter and younger

hypha (text figure 2, *4b*) is already binucleated. The shortest hypha is the youngest and last formed of the three (text figure 2, *4c*). These hyphae all have a diameter of about 4 to 4.5 microns; the ascogone at this stage has a length of about 17 microns. The hyphae next to the antheridial stalk cell, as in text figure 2, *4b*, begins its growth immediately to the side of it, and is from the beginning in close contact with both oogone and antheridial stalk. It will therefore follow the groove whose course is the resultant of the contours of the oogone and the adjoining cell wall of the antheridial stalk. The antheridial branch, being considerably less in diameter, following the contour of the ascogone, forms a curve with a slightly lesser radius than that of the

Fig. 2. *3*. Germinating conidium with only one gnarled germ-tube and two germ-tubes which resemble the mycelium. *4–6*. Three successive serial sections of a young ascocarp whose two-nucleated ascogone has not yet been completely covered by the initial envelope. *4a*, Antheridial stalk cell; *4b*, bi-nucleated enveloping hypha; *4c*, youngest of the three enveloping elements; *5a*, antherid with part of the stalk-cell; *5b* and *c*, enveloping hyphae. *7*, *8*. Two successive serial sections of a young ascocarp in which the initial envelope is complete and the hyphae which will form the second layer are pushing up between the two-nucleated ascogone and the initial envelope.

ascogone. The next branch will follow the perithecial wall. In general we may say, however, that the number of enveloping hyphae is seven or eight, and that apparently each hypha divides transversely but once, forming thus 14 or 16 cells. These cells are ultimately of approximately equal size, about 20 microns long, and 5 microns in greatest diameter (text figure 3, *17*), so that there are about sixteen somewhat similar cells in the first layer of the perithecium.

These cells constitute what we may call the initial envelope of the young ascogone. In spite of variations it seems to me that we can recognize elements and processes which are typical in the development up to this stage and that the considerable range of diversity in a series of young ascocarps is to be considered as a matter of morphotic modification.

The type process then may be conceived as consisting in the development of five enveloping hyphae arising simultaneously from the basal cell of the ascogone (text figure 2, *5* and *6*) and two from the basal cell of the antherid (text figure 2, *4*). Such a typical stage taken from living material is represented in text figures 4, *19–21*, and 5, *18*. The hyphae thus form a palisade of similar cells about the ascogone, the older previously formed antheridial stalk cell forming part of the series. These hyphae would typically all reach the antherid at the apex at the same time, and the initial envelope would consist of a palisade of similar cells about the ascogone. De Bary's (1863) figure 11, plate IX, for *Erysiphe* suggests such a type. If each of these cells now divides once in its middle and then expands laterally with the growth of the ascogone, we should have 16 truncated pyramidal cells. If there were as many as nine or ten original enveloping hyphae, the initial envelope would consist of eighteen or twenty cells.

No two perithecia are entirely alike in the arrangement and shape of their peripheral cells at maturity. The ultimate number of cells in the outer layer of the mature perithecium is between 18 and 24, so that it is clear that there is little cell division once the ascogone is covered, and probably some of the first-formed 16 cells do not divide further.

Whether the additional cells arise from further upgrowing hyphae or by division of the typical 16–18 cells is not clear. They grow in their tangential diameter with the growth of the ascogonium, the tangential expansion taking place at the expense of their radial diameters. Ultimately in the mature perithecial wall (text figure 5, *23*, *24*) they are plate-like, four-, five-, and six-sided or irregularly shaped cells. The cells are about 6 microns in radial diameter by 6 microns in tangential diameter when the three layers of the perithecium are complete; but when the ascocarp has reached maturity, they are generally 5 microns or less in thickness by 20–30 in tangential diameter. The average tangential diameters of the cells of the initial envelope are between 20 and 24 microns. The cells have increased about 12 to 15 times in volume.

The fertilized egg nucleus divides very shortly after fusion, and the two daughter nuclei separate slightly (figures 15 and 16) and come to lie in the upper part of the ascogone (figure 17).

At this stage the ascogone is not yet completely covered and the cells of the initial envelope have not yet begun to flatten. This binucleated stage of the ascogone is apparently of rather long duration, since the greatest growth and development of the perithecial cells takes place during this period. The ascogone does not increase noticeably in diameter, but elongates considererably during the binucleated stage, the elongation apparently taking place in the lower end while the nuclei remain in the upper end (figure 17). The ascogone, which at the beginning of the formation of the initial envelope measured between 8 and 10 microns in thickness, remains so up to the four-nucleated stage, but it elongates from 18 to 30 microns. The ascogone elongates with the growth of the enveloping hyphae. However, as it becomes enclosed at the upper end with its further elongation, it becomes curved. The initiation of this curvature

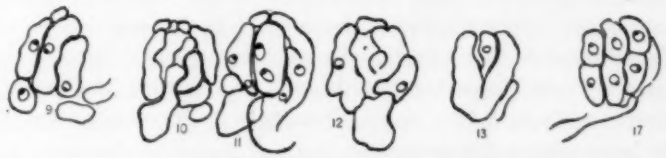

Fig. 3. *9–13*. Five successive serial sections of a young ascocarp showing the typical, irregular habit of growth of the enveloping hyphae after the initial layer is complete. *17*. External view of the initial envelope; each hypha has divided once.

may take place very early, as noted above. Its further development is, however, very plainly a matter of the interplay of two factors, first, its own growth in length and, second, the resistance offered by the cells of the primary envelope. It is obvious that less resistance is offered to lateral expansion with the assumption of a globular form than would be offered to further elongation into a cylindrical form. The position of the apex of the ascogone is for a time at least fixed by its adhesion to the antheridial cell. The stalk cell of the antherid, after its function is completed, apparently does not elongate further. The result is the curvature of the elongating ascogone in such a fashion that the centre of its convex surface comes to point vertically upward and thus fixes the location of the spatial center of the future ascus.

Figure 20 represents an ascogone similar to the one represented in figure 22, but this figure shows it rotated 90 degrees on

its vertical axis. The base of the ascogone is decidedly narrowed, and suggests that the vegetative hyphae may exert considerable pressure in this region.

This narrowing of the base of the ascogone begins to appear after the first layer of the perithecial hyphae is complete (figure 17), and from the general appearance of this region it appears as if the ascogone were wedged in on all sides. This constriction becomes more pronounced, until the base has the form of an inverted cone (figures 20, 23). However, the constriction of the base of the ascogone is not always so pronounced and often appears to be quite wanting (figures 18, 21, and 22).

When the primary envelope has completely enclosed the ascogone, a second layer of hyphae begins to develop between it and the ascogone. The hyphae that form the inner layer arise from the basal cell, alternating with those of the ascogone (figures 16 and 18), and appear to wedge their way between ascogone and primary layer, becoming, as a result, somewhat wedge-shaped at their ends. In pushing upward these hyphae force the outer layer outward and away from the ascogone (figures 13, 16 and 18), so as ultimately to form a second complete layer about the ascogone.

The antherid and its stalk cell, which in the beginning were part of the initial envelope, have become a permanent part of this layer, and are separated with it from the ascogone by the intercalated secondary layer. In figure 19 the elongated antheridial stalk cell may be seen as part of the outer wall of the perithecium, the empty antherid in this case being lifted entirely above the ascocarp. This is a common appearance. The old antherid very frequently appears as though the enveloping hyphae had forced themselves under it (figures 13, 18, and 19).

With this stage the rudiments of the cortical layer are in the main complete. The ascocarp at this stage, when the two first layers of the perithecium are complete, has an outside diameter of about 35 to 40 microns (figures 18, 20, and 21). The perithecium seems to expand more rapidly in its diameter than the ascogone grows in size, so that there is a tendency to leave vacant space between the two.

Development of the sex cells, the ascogone, and the ascus

After the mycelium has reached a certain stage of maturity, the sex cells develop. They tend to grow upward, away from

the leaf surface, at angles varying around 90 degrees. They rarely stand at exactly 90 degrees to the host surface; commonly they are about 60 degrees and occasionally at 45 degrees to the substratum. I find no evidence that these cells in their growth react in any way to light or gravitational stimuli. The mildew, as stated above, is either epiphyllous or hypophyllous, and the leaves are inclined at varying angles to the sunlight. The sex cells of *Sphaerotheca* show equally varying positions, whether on one side or the other. Negative response to moisture, hygromorphosis, may be concerned in determining their general positions.

The distribution of the sex cells on the mycelium illustrates perfectly the conception that sexual reproduction is the expression of what we crudely call maturity in the life cycle of the mycelium. The sex cells are formed from hyphae about six microns in diameter, when the mycelial patches are a millimeter or more in diameter, and they appear successively as the mycelium spreads and the hyphae attain a certain maturity. At the time the sex cells appear, the hyphal cytoplasm is homogenous and only very slightly vacuolate. The assumed physiological changes of sexual maturity come to expression as a difference in staining reaction, both between antherid and oogone and between them and the vegetative hyphae.

The antheridial branch in my preparations is always in advance of the oogone in development (figures 1, 2, 3, 4, 5, and 6), or rather is always longer, for the total volume of the two cells seems to be about the same. In the stage represented by figure 5 the average dimensions of the oogones are about 7 by 15 microns, of antherids 5 by 25. The two branches adhere closely, and often it appears that the more rapidly growing antheridial branch tends to bend the oogone to one side. The preparation represented in figure 3 clearly illustrates this point. Since the oogone does not keep pace with the more rapidly elongating antheridial filament, the two bend toward the oogonial side. This may explain why the oogone and the ascogone are also so commonly inclined at an angle less than 90 degrees to the leaf surface. The study of living material shows that even the very young stages are generally at such an angle.

I am inclined to believe that the curve in the oogone, the bending over upon itself in the later stages of its development

before the formation of the ascus, is initiated by this curvature of the oogone. I shall discuss this later on.

The antheridial branch is about twice the diameter of the mycelial hypha from which it arises, and appears as an elongated, stout, somewhat pointed cell, closely appressed to the oogone and growing in the same direction with it (figure 1). The single large nucleus that is at the base of the branch divides, and a wall separates the sister nuclei, which are now about one-half the size of the original nucleus, and one remains in the newly formed basal cell (figure 3), while the other migrates to the upper part of the branch where another division takes place. The resulting nuclei have about one-half the diameter of the original nucleus of the antheridial cell (figures 5, 6, 7), though the upper one is considerably smaller and migrates to the very tip of the cell where it is cut off by a wall (figures 5, 6, 7). The resulting uni-nucleated apical cell becomes the antherid. Thus three uni-nucleated cells are formed, a small, oblong, somewhat cap-like cell, the antherid (figure 7), a longer portion whose protoplasmic content is homogenous and tends to stain more densely than that of the other cells (figure 7). The antheridial stalk cell is rather stout in the middle and tends to taper at each end with the nucleus in the middle (figures 7, and 10). The basal cell is decidedly vacuolate (figure 6). The whole filament closely follows the contour of the oogone and its tip, the antherid, lies more or less on the apex of the latter (figure 5, 7, 10). Occasionally the antherid is placed a little to one side of the apex, as shown in figures 8 and 11.

The oogonial branch is generally about three times the diameter of the hypha from which it arises, and appears as a short, stout, somewhat ovoid uni-nucleated branch. Occasionally an oogonium appears slightly narrowed towards its apex, as in figure 4; but I am not certain that this is not due to the treatment by fixatives. The oogonial branch contains near its base a single large nucleus, which is about 5 microns in diameter, slightly larger than that of the nucleus of the branch destined to produce the antherid (figure 1). The oogonial nucleus divides, and a wall separates the daughter nuclei (figures 2, 3). The cross wall is marked by a slight constriction and is placed about one-third of the distance from the base of the oogonial branch to its apex (figures 2, 3, 4). The upper two-thirds of the branch becomes the oogonium, which at this stage is markedly turgid,

ellipsoid, and thin-walled. The cytoplasm of the oogone at this stage may be homogeneous or very finely granular, and shows no vacuoles; but the basal cell begins to show very small vacuoles, even at this early stage, and its cytoplasm is less homogeneous (figure 6). The nucleus of the oogone is considerably larger than that of any other cells of the group, measuring about 3.5 microns. The oogonium now bulges slightly at the apex, forming a papilla. The bulging region shows a strong affinity for the red stain of the Flemming triple stain. With Unna blue it stains very deeply, appearing very dark blue even in otherwise weakly stained preparations. It seems probable that there is a gelatinization of the walls between antherid and oogone in this region. Preparations of a stage a little later show a comparatively thick cell wall in this region which stains very dark red and again suggests that the wall is gelatinous at this point.

Fertilization is accomplished by the breaking down of the adjoining walls of the antherid and the oogone, followed by the entrance of the male nucleus into the oogonium and ultimately the fusion of oogonial and antheridial nuclei. The pore is most clearly visible when the antherid and oogone are viewed from the side (figures 8, 10). The cytoplasm of the two cells is seen to be continuous, though there is no evidence that the entire contents of the antherid is emptied into the oogonium. Only the antheridial nucleus migrates into the oogonium, where it moves immediately to the female nucleus.

In figure 5 the sexual cells are complete, and fusion is about to take place. The region of fusion shows the characteristic staining reaction. In figure 8 the fusion pore is distinctly seen in section, the cytoplasm of the one cell is in contact with that of the other, and the small male nucleus, which is just within the oogonium, has apparently just entered it. In figure 9 the male and female nuclei are lying side by side, and are about to fuse. Which of these two figures represents the older stage, I am unable to say. The cells shown in figure 14 are larger, and one of the first of the enveloping hyphae is beginning to grow from the basal cell. It may therefore be considered the older. The two nuclei are now about equal in size, the antheridial nucleus having grown slightly (figure 9). Both male and female cells are in this case considerably smaller, and they may be regarded as in a slightly earlier stage than that shown in figure 14. In figure 11

the two nuclei have fused completely; the nucleus here is about 5 microns in diameter, having apparently about twice the combined volume of the two figures in figure 14. In figure 10 are represented a pair of larger sex cells, in which the sexual nuclei have already fused. The fusion nucleus here has a volume about equal to that of the volume of the two sexual nuclei represented in figure 14. Figures 12 and 9 may represent successive stages of a smaller pair of sex cells than those represented in the figures 10 and 14. Such figures merely represent variations in size of the gametic pairs. A figure like that represented in figure 12 would never in the immediately following stage look like the one represented in figure 10.

The fusion nucleus now undergoes a division resulting in two equal-sized daughter nuclei, and a rapid growth of vegetative hyphae about the two-nucleated ascogonium takes place.

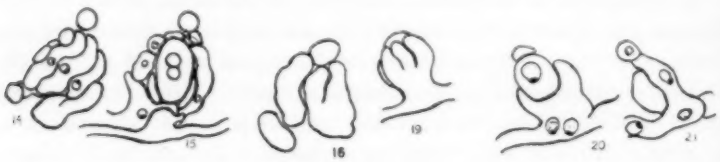

Fig. 4. *14–16.* Young ascocarp showing irregular development of the perithecial wall. In *14*, there is a slight tendency of the hyphae to form a spiral pattern. *19–21.* Successive sections of a one-nucleated ascogone with more or less uniformly developing enveloping hyphae.

The two nuclei of the ascogone during the development of the perithecium divide once so that there are four at about the time when the third layer of the perithecium is complete (figure 24). I am of the opinion that these nuclei arose by a simultaneous division of the two nuclei in the ascogone. I have never found a distinct three-nucleated ascogone but have many preparations which show four nuclei in the ascogone and many preparations which show ascocarps at about the same stage of development as the four-nucleated ones but with only two nuclei in the ascus. It is therefore very probable that the four-nucleated immediately follows the two-nucleated stage, the nuclei dividing simultaneously. Cross walls then separate the terminal and basal nuclei from the middle pair in the ascogone. There thus results a column of three cells, of which the middle one is binucleated and

develops to form the ascus. The binucleated central cell, the penultimate cell, is in the region of the ascogone in which the bending takes place (figure 25), so that from the outset it bulges out much more on its convex side. It expands very rapidly and soon becomes short and pear shaped (figures 26, 27, and 29).

The two nuclei in the penultimate cell move together (figure 25) and fuse (figure 26), forming the definitive nucleus of the ascus. Figure 26 represents a young ascus showing the fusion nucleus in which the nucleoli have not yet fused. The young ascus at this stage has a diameter of about 15 to 18 microns, the diameter of the whole ascocarp being around 40 microns. After nuclear fusion the ascus continues to expand very rapidly, apparently in every direction (figures 26, 27, 28), and the nucleus enlarges with it. In the beginning the nucleus is elongated, appearing to be drawn away from its basal position (figure 27). The ascus apparently becomes very turgid to conform, in spite of the irregularities in the perithecial cells and its original shape, to a least surface configuration. At its base the young ascus tends to remain narrowed as though pinched by surrounding cells for a considerable period (figures 26, 27, and 29), and in some cases this pinched condition is never entirely lost. The ascus grows rapidly and symmetrically against the pressure of the perithecial wall. Its basal portion is the last to round out and lose its blunt-pointed shape. Many asci do not become spheres, but remain slightly dorso-ventrally flattened, appearing oval in section (figures 33, and 35).

The cell wall of the ascus is very thin up to the time the spherical shape is attained, but after this there is a gradual thickening as maturity is approached. In the stage shown in figure 30 the cell wall is shown as very much thickened.

Further growth and ripening of the perithecial envelope

The inner zone of the perithecial wall develops between the ascogone and the second layer and apparently arises largely by growth of the cells of the second layer (figure 29). That is, we now have a beginning of radial growth inwardly from the envelope toward the ascogone. In figure 22 the two elongated cells in the lower right-hand side of the figure have the appearance of having elongated radially and are about to divide. Immediately above these two cells are a short and a long cell which apparently

are the result of division of a single elongated cell. Possibly the two cells below will divide similarly, and in this manner the innermost layer of perithecial cells may arise. The third layer, as noted, begins to develop at a time when the curved ascogone does not completely fill the perithecial wall. Its cells at first push into the spaces around the ascogone and show no tendency to tangential flattening. Later, when the ascus begins to swell rapidly, they are pushed back so as to form a layer of cells of fairly equal size and constant shape (figures 31, 33, and 35). On the right-hand side in figure 22 there are three cells of the inner layer which, because of their narrowness and obvious connection with the basal cell, appear to have arisen by upgrowth from it and not by ingrowth from the secondary layer. The innermost layer of cells arises both by transverse divisions of the ingrowing branches from the second layer and in lesser degree by further upgrowth from the basal cell. The ingrowing branches would typically tend to become cylindrical hyphae, but they take on such shapes as their position permits. Ultimately they are irregularly polygonal in tangential aspect and irregularly quadrilateral in radial section (figure 29). The ascocarp shown in figure 31 has almost reached its maximum size, and the cells of the outer layer are beginning to approximate their ultimate plate-like form. The inner cells are still large and isodiametric, and interhyphal spaces are present. The whole perithecium in this figure has about the number of cells commonly found when the ascocarp is mature, and probably there is no further increase in the number of the perithecial cells after this stage. With this stage the growth of the perithecium is complete, and its further modifications are those of differentiation and specialization.

After the nuclear fusion the young ascus grows very rapidly, the ultimate cell and the stalk cell of the ascogone become part of the inner layer of cells of the perithecium. These cells of the ascogone remain distinct for a time, as is shown by their different staining reaction (figures 29, 31, 34 and 35); but when the ascus expands their identity is lost and they can no longer be distinguished easily from the other cells of the inner layer.

The cells of both the outer cortical layers of the perithecium now begin to show changes in their appearance. The cell walls become slightly thickened and the contents vacuolated. I am of the opinion that after this stage they no longer divide, the

ultimate number of cells between 18 and 22 being reached at this time. As the cells grow tangentially they leave no intercellular spaces between them. The hyphal cells adhere very closely and are in intimate contact throughout. They form a strong limiting layer against which the inner cells are flattened by the inflating ascus. In figure 35 the ascus has expanded considerably beyond the size shown in figures 27 and 29, and the cells of the inner layer are becoming flattened radially. Ultimately the ascus obviously develops a high turgor pressure which flattens the cells of the softer inner layer so that they become quite thin (figures 33 and 35).

These inner radially growing cells of the perithecium retain their protoplasmic contents even to a very late stage, when the

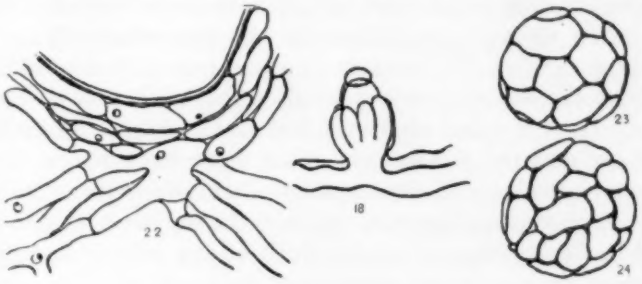

Fig. 5. *22.* Base of a mature ascocarp raised from the leaf surface by the appendages. *18.* Asocogone with palisade of enveloping hyphae growing uniformly upward. *23, 24.* Apical views of mature ascocarps showing the typical patterns of the perithecial cells.

spores are completely developed. Even in early stages they have a different staining reaction from that of the wall cells and doubtless they have a different function. They are large and rounded in the beginning and decrease in size with the growth of the ascus. The natural suggestion is that they are nurse cells for the ascus, as was noted by Harper (1895), and always remain thin walled.

The basal cell of the ascogone in these later stages is still clearly differentiated from the surrounding cells, and there is apparently a definite functional connection between the ascus and the stalk cell of the whole ascocarp (figure 31). It is, however, possible that after the ascocarp has reached its maximum diameter there is no further absorption from the substratum,

the ascus growing at the expense of the perithecial cells—probably the inner nurse layer.

During the earlier stages, when they are still large and isodiametric, the cells immediately surrounding the ascus are regularly uni-nucleated; but later, when the ascus has taken on its illipsoid shape, these cells become bi-nucleated to tetranucleated. The cells of the two wall layers also contain one or two, rarely three nuclei in fully developed ascocarps.

The appendages begin to appear when the three layers of the perithecium are complete. They arise from the outer layer of cells in the basal region of the perithecium. They are eight to twelve in number and are long (300 to 400 microns), nucleated, tortuous, and hyphae-like. Occasionally an appendage is branched. They interweave with the vegetative mycelium, and it is often difficult to distinguish the appendages from this mycelium. When the ascocarp is mature, it is often seen lifted up above the leaf surface to a height equal to its own diameter. Apparently it is raised above the leaf surface by the appendages which are directed downwards at an angle (text figure 5, *22*). There is no evidence of any special mechanism in the appendages which serves to raise the ascocarp from the leaf surface, such as is found in *Phyllactinia*. Apparently it is due to the downward growth of the numerous appendages.

Epiplasmic inclusions

I first observed highly refractive, conspicuous granules in the ascus of *Sphaerotheca castagnei* in material fixed with Allen's modification of Bouin's fixative. These granules stain bright ultramarine blue with the triple stain. In very late stages they stain red. Merkel's fluid, Herman's fluid, picroformol, plain Bouin and Allen's Bouin give preparations in which the granules appear bright blue when the triple stain is used. With Flemming's fixing solution such granules do not generally appear, though occasionally hyaline, refractive granules resembling them in shape, number, and location may be found. It is probably because of the very widespread use of Flemming's fixative, in which the granules are scarcely if at all differentiated, that they have hitherto been overlooked in the mildews.

Unna's polychrome blue, when used with Allen's Bouin, Merkel's or plain Bouin fixative, gave varying results. The

granules usually stained a deep violet, purple or reddish purple color, though sometimes they showed pale blue or greenish blue and occasionally would take no stain (figure 34) at all, even though other parts of the ascocarp showed well stained granules. While the granules frequently exhibited very distinct metachromasy with Unna blue, I have never obtained with this dye the bright red granules described by Guilliermond (1904) for the granules in the asci of *Aleuria cerea*, *Helvella sulcata*, etc.

The perithecial cell granules are very small, numerous, and purplish in color with the Unna dye, and appear long before any granules become visible in the ascus. These are quite different in appearance from those which later develop in the ascus, remaining small, very dense and staining dark blue with Unna blue even in very late stages, while those in the ascus become very large, less numerous, and not so dark in color.

No such granules appear in any of the cells at very early stages of the developing ascocarp. Only after three layers of perithecial cells are formed do they begin to appear, the first ones becoming visible in the innermost cells (figure 28). The perithecial cell granules are fairly numerous from the beginning and become several times larger and more numerous in later stages (figure 33). The epiplasmic granules do not appear until after nuclear fusion. Here again they are numerous from the beginning, becoming more numerous and larger as the ascus increases in size. The granules appear to be formed only after a cell has reached a certain stage of development. In cells that have just divided no granules are present, as for example in certain cells surrounding the penultimate cell represented in figure 28. Here certain cells of the third layer have no granules, while others have extremely minute, barely visible granules. The perithecial cell granules in the second and first layers are larger and more numerous, while the penultimate cell has none. It is difficult to ascertain from my preparations how these granules arise in the cells.

The epiplasmic granules, even in the early stages, are found each lying in a clear area in which they are eccentrically placed and increase many times in diameter as development proceeds, from particles barely visible with highest magnification to those as great as seven microns in diameter. When the ascus has reached its maximum diameter, the granules are from three to six microns in diameter and appear to fuse (figure 33). The

fusion appears to be merely a physical result of their coming in contact through an increase in their diameter and perhaps through cytoplasmic movement. The largest granules appear in the ascus during the uni-nucleated stage, when certain of them may attain a diameter of ten microns. After the first division of the ascus nucleus during the two-nucleated stage, there are present numerous small epiplasmic granules varying in dimensions but below 2.5 microns or very rarely 3 microns in diameter (figure 30). Such granules vary in their staining reactions; some become red, some blue with the triple stain, though all appear to stain blue when the treatment with safranin is very brief. If these granules are similar to those in the immediately preceding uni-nucleated stages, it is difficult to understand how the abrupt change in their size takes place. Large granules occur in all the late uni-nucleated stages but the immediately following bi-nucleated stages have the small granules. Throughout the four- and eight-nucleated stages as well as in certain eight-spored stages the small epiplasmic granules persist.

In stages in which the outer perithecial cell walls are brown and the protoplasts extremely vacuolated, large irregular pale blue masses, from eight to fifteen microns in diameter with from one to four dense, dark blue, spherical centers and resembling several fused, large granules of the kind found in uninucleated asci, are present in the epiplasm. They appear to be aggregates of large granules and may arise as Bunge (1895) described by the fusion of other granules. In addition to these, many small granules like those described are also present in the epiplasm as well as in the spores (figure 35).

Similar granules are common in young hyphae. In conidiophores and conidia, as well as in the germ tubes of the latter, granules of similar appearance are also frequently present.

In still later stages large, often irregular granules, six microns in diameter, both red and blue in the triple stain, occur in the epiplasm. These are probably degeneration products and unlike any of the granules described above.

In the fusion nucleus of the ascus granules similar to those in the epiplasm occur (figure 27). I have not found them in any other nuclei of the ascocarp, the large nucleus in the ascus being the only one in which they are definitely recognizable.

In the ascus during the uni-nucleated stage, the epiplasmic

granules are indiscriminately scattered in the epiplasm. There is not the slightest tendency for them to be localized at any time, either about the nucleus or in any other region of the ascus. They present no evidence of connection with or origin from the nucleus or through its agency. There are commonly, as noted, both large and small granules within the nucleus, but these are not generally in connection with the chromatin. Guilliermond's (1903) suggestion that the granules may be formed as a result of secretions from the nucleus or that they are secretion products from the chromatin finds no support from my study of *Sphaerotheca*.

Judging from their spherical form, the granules are liquid or semi-liquid substances chemically different from the surrounding epiplasm. They arise perhaps as very minute droplets secreted by the cytoplasm.

DISCUSSION

In the light of the specificity in host relations found in the mildews of P. Magnus (1898), Salmon (1904), Steiner (1908), Reed (1908), Woronichine (1914), and others and of the morphological variations which have been reported as occurring in single species, as recognized in Salmon's monograph, I am of the opinion that further study may lead to the recognition of many of the current biological races of mildews as varieties or even species. Woronichine has already reported variations in the dimensions of ascocarps, asci, spores and certain sterile hyphae of *Sphaerotheca pannosa* on the rose and of *Sphaerotheca pannosa* on the peach and on the basis of both the physiological and morphological differences proposes to recognize them as distinct varieties.

The fact that on a particular host there may be two or more asci in a form which usually has but one ascus and that the perithecium which usually consists of but three layers occasionally has four or even five layers as well as other structural variations, shows the need of further study of the species question in these fungi.

Harper (1895) describes the ascogone in *Sphaerotheca* as consisting regularly of a column of five or six cells, while Dangeard (1896) figures only three. In my own preparations I find regularly three cells in the ascogone and in only one instance a four-

celled stage (figure 38) among several hundred three-celled ascogones. That such basic structures can so vary seems hardly probable, and the need of study of further forms is obvious.

Gäumann (1926) has suggested that the lack of agreement in the conclusions drawn from observations on the morphology and development of the mildews may be due to the fact that the studies were made on material from different host species.

The great similarity between the parenchyma of higher plants and the pseudoparenchyma of fungi is striking in view of the difference in the method of their formation. Parenchyma is formed by the growth and division of the cell in length, breadth and thickness. Pseudoparenchyma is formed by the growth, branching, interweaving, and adhesion of hyphal filaments.

The special relations between the cells in a parenchyma are determined largely by their method of origin, though the evidence seems to favor the view that the contact relations of the protoplasts may be dependent on the secondary development of plasmodesmen. The interrelations of the cells in the case of pseudoparenchyma are for the most part secondary and are achieved by thigmotactic responses and adhesion. Pits and presumably plasmodesmen are present and serve possibly as conductive channels through which morphotic stimuli are transmitted from cell to cell.

The problems involved in the distribution of the mycelium on the leaf of the host are doubtless analogous to those presented by the distribution of roots in the higher plants. It is hard to conceive that negative chemotactic responses involving repulsions are responsible for the generally radial direction of growth of the hyphae about a germinating spore. I have noted that the initial growth results in a generally radial arrangement of the main hyphal branches and that the typical appearance of the mycelium on an infected area of leaf is that of a radiating system of hyphal filaments. According to Nöll (1900) the radial direction of growth of secondary plagiotropic roots after the removal of an interposed barrier is due to morphaesthesia. According to this conception the main orienting factors in hyphal growth would be matters of rectipetiosis. Further observations should be made to test this and other hypotheses as to the factors which determine the growth directions of the hyphae on the leaf.

The differences in the staining reaction between the sex

cells themselves and between them and the vegetative hyphae suggest physiological differences which may be chemical in nature. Whether these changes should be classed as rectipetioses is to be determined perhaps by Pfeiffer's (1925) limitations of the conception. Pfeiffer holds that the internal morphotic factors operate as specific substances which are produced by the tissues and are carried from cell to cell or through conducting channels to more distant tissues whose growth forms may be thus determined. The difference in staining reaction in the sex cells, as described above, may possibly be an indication of the formation of such specific substances.

It is evident that carpogenesis is initiated by fertilization, and it is natural to assume that the latter process involves the formation of specific substances which act as stimuli in initiating the outgrowth of the hyphae of the primary envelope. Such stimuli may be classed as carpogenic factors. The substance may be of the nature of hormozones in Gley's (1911) sense and in a morphogenetic sense may be called morphones.

The development of the perithecial wall does not generally begin before the fusion of the sexual nuclei, but I have found some cases in which the enveloping hyphae bud out before this stage. Such precocious development indicates that the stimuli to carpogenic development may arise before cell fusion occurs. The case represented in figure 13 is unusual. Fertilization does not yet seem to have taken place, but the enveloping hyphae are sprouting from the basal cells of both antherid and oogone. In figure 13 the hyphae are shown as already growing from the basal cell, yet fertilization has apparently not yet taken place. The antherid is gradually being pried away from the oogone by the hyphae which are pushing up between it and the initial envelope. That in this case an antherid is being pushed away from the oogone is possible. The antheridial filament is always more advanced in its development than any other hypha of the ascocarp, and typically occupies a position similar to that represented in figure 13. The case may be one of delayed or abortive fertilization in which perithecial development has none the less continued. It is to be noted that the oogonial nucleus in this case is unusually large and has not divided. Possibly figure 37 represents a still later stage of a similar case in which the large oogonial nucleus has still not divided, while perithecal development has gone on independently.

As noted, I have not observed the spiral pattern of the initial envelope of the ascogone regarded by De Bary as characteristic, and I am of the opinion that it is at least unusual and results only when there is a very rapid uniform development of the enveloping hyphae (text figure 4, *14*). The explanation of such a pattern is probably analogous to that generally accepted for the spiral twist in the enveloping cells about the egg of *Nitella;* that is, the combined transverse diameters of the enveloping cells are less than the circumference of the ascogone and their length considerably greater.

Several of Dangeard's (1896) figures are unlike any which I have observed. His figure 15a (p. 276, 1896) shows an oogone of two cells; figure 15d, a four-nucleated ascogone with little perithecial development; figure 15e is also unlike anything that usually occurs in my preparations. I have found occasionally some very unusual figures which in my opinion are abnormal, at least for the complete life history of *Sphaerotheca*. Some of these figures resemble certain of those of Dangeard, except that they are extremely large. Figures 36 and 37 are comparable to the four-nucleated stage represented in Dangeard's figure 14b, but in the former perithecial development has been inhibited. Figure 32 may represent a case in which the oogone has never been fertilized, yet has continued to grow. The filament (a) in figure 32 may be a degenerating antheridial filament which for some reason never came to maturity, possibly because it developed from an incompatible mycelium. The presence of two or three nuclei in the terminal cell of such a presumably unfertilized oogone is very peculiar and not easily explainable.

The stalk cell in these preparations (figures 32, 36 and 37) is in each case uni-nucleated. These naked oogones (they can hardly be called ascogones, since there is no assurance that asci ever develop from such structures) may on the other hand be looked upon as isolated oogones which have developed without the presence of antherids. The oogone in figure 13, where the male nucleus has apparently failed to enter the oogone, suggests the possibility that oogones and antherids may develop in contact and still fail to complete the process of fertilization.

The demonstration of the presence of a specially stained region of the wall of the oogone at the apex of the antherid suggests an analogy with the receptive papilla of *Pyronema*,

Albugo (Stevens, 1899), and certain algae, such as *Vaucheria* (Oltmanns, 1895), *Oedogonium* (Klebahn, 1892). I do not find a hyaline receptive spot in the cytoplasm beneath the stained area. It is the wall of the oogone apparently which becomes differentially stained as shown in figures 6, 10, 11, and 14.

In his studies on mildews Bezssonoff (1914) is in disagreement with earlier workers on several points. According to Bezssonoff the antheridial branch of *Sphaerotheca mors uvae* does not cut off a small uni-nucleated antheridial cell as in the species of *Sphaerotheca* described by Harper (1895, 1896, 1905), Dangeard (1896), Blackman and Fraser (1905), and Winge (1911); but the antheridial branch becomes bi-nucleated, the apical nucleus migrates into the oogone, and the remaining nucleus degenerates in situ. In *Microsphaera*, Bezssonoff claims to have a stage showing the passage of the male nucleus into the oogone, though his figure 3, plate VII, does not show this very clearly. The fusion pore differs from previously described fusion pores in the mildews in being at the extreme end of the area of contact between the antherid and oogone, their walls at this point appearing to form an almost straight line.

The initiation of perithecial development in the mildews by the formation of a circle of perithecial hyphae which grow out radially from the stalk of the ascogone, and the development between these hyphae and the ascogone of further series of hyphae, parallels in principle the corresponding stages in the development of the apothecial envelopes of *Pyronema* and other Discomycetes. The subsequent transformation of these vegetative hyphae into the variously shaped plate-like cells of the perithecium, the differentiation of the outer cortical layer into dark colored, thick-walled cells and the inner layer into thin-walled cells from which the nurse layer develops, are to be regarded as expressions of the most specialized morphotic responses so far described for any ascocarp. In the formation of the layers of pseudoparenchyma of the mature perithecium, two types of development may be recognized. The initial envelope and the inner perithecial layer may be regarded as at first a simple prosoplectenchyma which is developed symphyogenously. The mature paraplectenchyma (Lindau, 1899; p. 25; Gäumann, 1926) or pseudoparenchyma results from the transformations through thigmotactic responses of the prosoplectenchyma (Lindau,

Gäumann) into the compact mature tissue of the outer wall. I have never found any evidence of meristogeneous division at any stage in the development of the cleistocarp. The mature cells are variously quadrilateral, pentagonal, hexagonal or irregular in tangential section and very much flattened as a result of pressure from the growing ascus. Thigmotactic responses with radial pressure from the ascus are the dominant factors in determining their form.

The spherical ascus of *Sphaerotheca*, as compared with the club-shaped forms of the Discomycetes and the intermediate forms in *Erysiphe* and *Phyllactinia*, illustrate how pressure may modify the tendency to a least surface configuration. When in *Sphaerotheca* two asci are developed in a single perithecium they modify one another's form at their surfaces of contact so that the adjoining walls become flattened and the asci become approximately hemispherical. In cases where three asci are produced as reported by Salmon (1900), they probably assume a form analogous to that of the carpels of an orange. The more numerous the asci become, the greater must be their mutual lateral pressures and the more elongated and club-shaped is the form (see Harper's figure 40, plate XII, 1896).

The name nurse tissue is suggested for the innermost layer of the mature cleistocarp of the mildews because of its suspected connection with nutrition of the ascus, as indicated by Harper (1896 and 1905). Harper (1896) also suggests that this layer may be capable of swelling on taking in water, causing the ascocarp to burst through high turgor of these cells, in order to liberate the ascopores. The fact that this layer is soft and moist at the time of spore discharge and that the whole ascus sometimes slips out (Salmon, 1907) or is ejected forcibly (Smith, 1884) also suggests its connection with spore discharge. Possibly this layer functions during the growth of the ascus as a nurse layer and is later instrumental in bursting the cleistocarp.

The appendages in *Sphaerotheca* closely resemble in their origin the secondary mycelium probably present in most ascocarps and described by Harper in *Pyronema* (1900). The secondary mycelium in the case of the larger ascocarps doubtless functions in the nutrition of the later growth stages. For the relatively small ascocarps of the mildews, nutrition seems adequately provided through the stalk of the ascogone. De Bary

(1863), in his general description, states that secondary mycelium in the mildews is developed at an early stage. The morphological evidence seems to favor the view that the mildews are not primitive, but highly specialized in connection with their obligate parasitism.

With the acquisition of the parasitic habit and the reduction in size of the ascocarp, the secondary mycelium became nonfunctional. Obviously the appendages are to be regarded as vestigial secondary mycelium. There is no evidence that the appendages of *Sphaerotheca* ever develop haustoria. Their ends are in all cases free and undifferentiated. In forms of the Erysiphaceae in which the appendage endings are branched or otherwise modified they apparently are acquiring new functions. The highly specialized structure of the appendages of *Phyllactinia* is adapted for lifting the cleistocarp up from the leaf surface. This is, then, a case in which vestigial organs have become secondarily specialized and have acquired a very specific new function.

I feel deeply indebted to Professor R. A. Harper for his encouragement and valuable assistance in the preparation of this paper.

COLUMBIA UNIVERSITY,
NEW YORK CITY.

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Explanation of plates

All figures were drawn with the Abbe camera lucida. Figures 1 to 25, and figures 28, 34, 32, 36, and 37 are magnified approximately × 1200; all other figures are magnified approximately × 900.

PLATE 28

Fig. 1. Male and female branches.

Fig. 2. Later stage; the gametes are cut off from the basal cells. The cytoplasm of the oogonium is more dense than that of either the basal cell or the antheridial branch.

Fig. 3. The antheridial branch appears as if it had through more rapid growth pushed the oogonium to one side.

Fig. 4. The antheridial branch has completely overtopped the oogone.

Fig. 5. The antheridial cell is cut off from its stalk.

Fig. 6. The apex of the oogone shows a small densely stained area at the point of fusion with the oogone.

Fig. 7. An enveloping hypha is growing from the oogonial basal cell before fertilization has occurred.

Fig. 8. Antheridial nucleus has entered the oogonium; the pore has not yet closed.

Fig. 9. Stage just before conjugation. The male nucleus has enlarged and is about the same diameter as the female nucleus.

Fig. 10. Fusion has taken place; the conjugation pore has not yet closed and the densely stained area at apex of the oogonium persists.

Fig. 11. Shows the persistent densely stained area and large fusion nucleus.

Fig. 12. The enveloping hyphae in an early stage.

Fig. 13. Sex cells in an advanced stage in which the male nucleus has failed to enter the oogonium.

Fig. 14. Egg nucleus has divided; the densely stained area at the apex of the ascogonium is still present.

Fig. 15. Binucleated ascogonium with several enveloping hyphae growing from both male and female basal cells.

Fig. 16. Binucleated ascogonium with persistent densely stained area at the apex. Initial enveloping hyphae have completely covered the ascogonium and the second layer of hyphae is growing between it and the initial envelope.

Fig. 17. The hyphae of the initial envelope is cut up into several cells. The ascogonium has elongated slightly.

Fig. 18. The second layer is almost complete. Empty antheridial cell which has been pried off from the ascogonium by the enveloping hyphae is at the apex of the ascocarp.

Fig. 19. Empty male cell with its stalk embedded in the initial layer of the perithecium.

Fig. 20. An ascogonium with one very small nucleus and two equal sized larger nuclei, the latter are typical.

Fig. 21. Curved binucleated ascogone. The curve is perpendicular to the focal plane.

Fig. 22. Slightly older. The third layer of perithecial cells is nearly complete.

Fig. 23. Similar to fig. 21, but the ascogone is somewhat stouter.

Fig. 24. Both ascogonial nuclei have divided. The centripetal radial growth of the hyphae of the inner layer is shown.

PLATE 29

Fig. 25. Three-celled ascogonium. Stalk cell and basal cell are in the next section. The penultimate cell shows the two nuclei about to fuse.

Fig. 26. Fusion nucleus in the young ascus. The nucleoles have not yet fused.

Fig. 27. Young ascus with several small epiplasmic granules. The fusion nucleus shows several small blue granules.

Fig. 28. Young perithecium showing large granules in the older cells, smaller granules in the second layer and very few or none in the youngest the innermost cells. No epiplasmic granules are visible in the young ascogenous cell.

Fig. 29. The inner, nurse layer, is complete. The cells are large, inclined to be quadrilateral in section.

Fig. 30. Eight-spored ascus with numerous very small epiplasmic granules.

Fig. 31. Perithecium reconstructed from two sections. The basal cell is connected with the ascus stalk cell which contains four nuclei. The nurse layer has become considerably flattened by the growing ascus.

Fig. 32. Presumably a two-celled ascogone in which fertilization has failed to take place; enveloping hyphae have failed to develop.

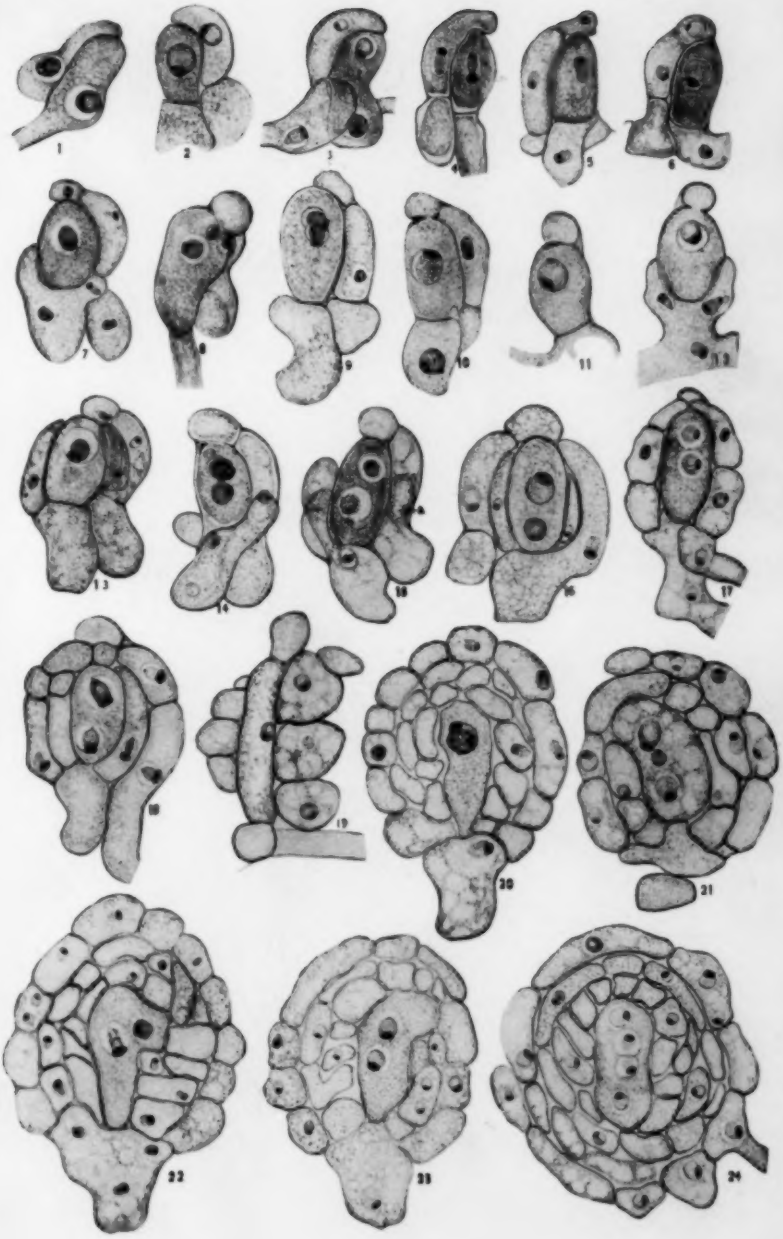
Fig. 33. Later stage than fig. 31. Large blue epiplasmic granules in the ascus, and small dense granules in the outer cortical layer.

Fig. 34. Similar to 33, but stained with Unna blue. The epiplasmic granules remain unstained while the perithecial cell granules appear deep violet in color.

Fig. 35. Eight-spored ascus with thick, apparently gelatinized, wall. Large dark blue masses containing denser spherical bodies.

Figs. 36 and 37. Stages similar to fig. 32. Fig. 36a shows what might be an undeveloped antheridial branch.

Fig. 38. A four-celled ascogone with fusion nucleus in the young ascus.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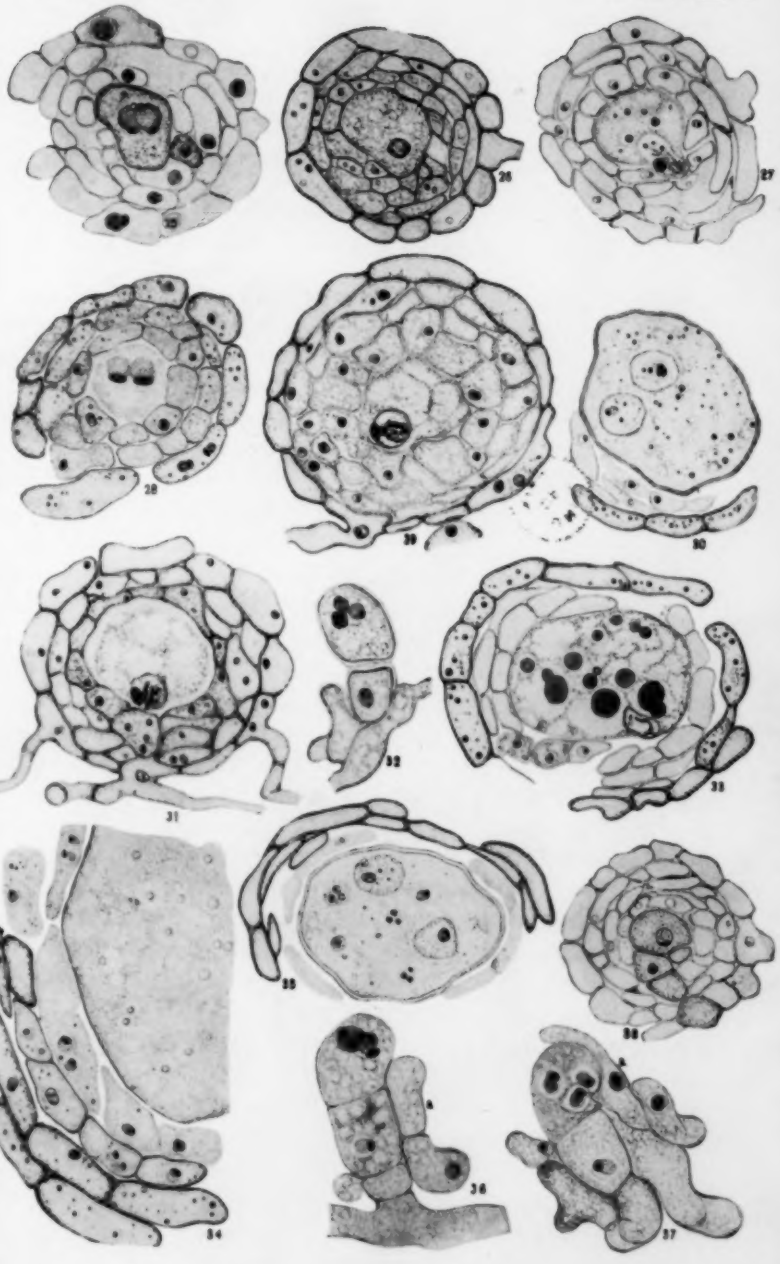

A contribution to the biophysics of Podophyllum petioles

WALTER J. HIMMEL

(WITH FIVE TEXT FIGURES AND PLATES 30, 31)

The effect upon growth of such external factors as pressure and tension has been studied by a number of workers. While it is apparent that such agencies as gravity and wind may alter the shape of stems and in some cases have altered their internal structures, yet there is a question as to whether these agencies do alter the rate of growth and the rigidity of axial organs such as stems, petioles, roots, and hypocotyls. In this connection the mechanical forces involved in the growth and curvature of such structures deserve consideration.

A knowledge of the effect of pressure and tension on growth, and the mechanical forces involved in growth, is highly important not only in explaining the behavior of plants in their tropisms but also because during normal or pathological development the cells of a multicellular plant must affect each other not only by chemical secretion but also by the mutual stresses and strains within a growing tissue. This study therefore has a direct bearing on the problem of cellular interaction during ontogeny.

Hegler (1893) investigated the influence of tension upon growth by means of attaching a thread to the tip of the shoot, passing it over a pulley, and fastening it to a weight at its free end. He found that the tensile strength of such stems increased with increased tension. In repeating these experiments Ball (1904), a student of Pfeffer, found that the breaking strength of a plant does not increase in response to a gradually increasing pull.

Pfeffer (1893) later found that the primary root of a bean seedling embedded in plaster of Paris develops a pressure of 100 to 140 grams, often sufficient to burst the cast. Later with a spring-dynamometer he determined that the pressure thus developed overcame a resistance of 352.7 grams or 19 atmospheres. He also found that resistance applied in this way caused production of mechanical tissue.

Brush (1908) found that contact has a decided strengthening effect upon the tendril of *Passiflora caerulea* and by the addition of tension a still greater strength is obtained.

In working with the woody stems of *Robinia Pseudo-Acacia*, *Rhus glabra*, *Populus tremuloides*, and *Ricinus communis*, Pennington (1910) found that there was no increase in mechanical strength under the influence of longitudinal compression. In young herbaceous stems of *Helianthus annuus*, *Vicia faba* and *Phaseolus vulgaris* he found that the development of mechanical strength was somewhat retarded by longitudinal compression caused by a heavy weight. He states further that neither light weights nor heavy weights have any appreciable effect upon the growth and strength of herbaceous stems which have already formed a cylinder of woody tissue.

The application of other pressures than that of longitudinal compression have been studied in their effect upon growth. Andrews (1922) has shown that a water pressure of 600 atmospheres reduced the growth of *Zea Mays* seedlings on the average to only a small fraction of the growth rate of the normal plants.

Pressure seems to affect certain chemical phenomena and thereby to have some influence on the energy relations of tissues. Meldolesi (1921) found that the action of pepsin and trypsin upon blood albumen was influenced by a pressure of over one atmosphere of CO_2 and N_2. The reaction was most rapid at a pressure of 5 atmospheres, less at 10 atmospheres, but more than at one atmosphere. The hydrolysis of arrow-root starch by diastase was also influenced by pressure in the same way as was the action of pepsin and trypsin.

Not many studies have been made upon the amount of work done by plants in growth. Cremieu (1923) has recently estimated the work done in growth by oats. According to his calculations 125 kgm. of oat seed planted on a hectare of ground lift during their development into mature plants 1500 kgm. of seed and 300 kgm. of straw to a height of 0.6 m.

MATERIALS AND METHOD

The so-called sterile shoots of *Podophyllum peltatum* used in this investigation have been shown by Holm (1899) to be peltate leaves. They are very suitable for investigations on the effects

of pressure because of their firmness, the absence of lateral appendages, and because the region of elongation, unlike the delicate meristems of true stems, extends from near the distal end to near the middle of the petiole. In determining this region several petioles were marked at 10 mm. intervals and several at 20 mm. intervals. After several days the intervals were remeasured. Only those of the upper half of the petiole were found to have elongated. As an illustration of this elongation the following figures represent the successive intervals in mm. from the distal end of one petiole after several days growth: 20, 25, 29, 33, 21, 15, 10, 10, 10, 10, 10. A fourth advantage of this structure for such studies is that the weight can be placed directly on the top, without tying anything to the petiole.

The growing season of *Podophyllum* in any given locality continues only for a few weeks. It was found possible to secure actively growing petioles at other than the natural season both by breaking the dormancy early and by delaying development. The rhizomes bearing dormant buds were dug up in the summer and autumn and transplanted into flower pots. These pots were submerged in soil on the north side of a building and after exposure to considerable cold weather during the winter were brought into the greenhouse during the latter part of January, where the buds began to open within two weeks and in about another half week reached the stage suitable for use in the experiments. During February rhizomes were also chopped out of the frozen soil in the woods, covered with sand, and transferred to a refrigerator where they were kept at a constant temperature of about 1° C. until after the normal growing season had passed. As needed they were removed from cold storage, potted in flower pots, and placed in the greenhouse where they developed more rapidly than either the normal or the preseasonal material. Usually the buds of these plants opened in a day or two and were ready for experimentation within a week. In this way the length of the season was extended from 8 weeks to about 16 weeks.

In attempting to measure the mechanical forces involved in the growth and curvature of stems and stem-like parts of plants, and the maximum energy which the plant is capable of so expending, three groups of experiments were prosecuted. In the first group longitudinal pressure was exerted by placing on the

apex of the plant a light weight (about 25 grams) and periodically increasing this weight by equal increments as long as the plant continued to raise it. The rate of elongation was recorded twice daily, and after elongation had ceased, the bending strength of the petioles was determined and also the amount of work done in raising the weight calculated. In the second group of experiments the petioles of plants were flexed back and forth in one plane alternately on either side of the vertical. This process of repeated bending, which may be given the name of flexation, was continued for several days, and as the plant elongated, the amplitude of flexation was correspondingly increased. After elongation had ceased, the bending strength of the petioles was determined in the direction of flexation and in the plane at right angles to it. In the third group of experiments plants were placed horizontal, and the energy which they are capable of expending in tropic response to gravity was measured.

ELONGATION UNDER PRESSURE

Rate of elongation

The pots containing the plants were placed in large saucers filled with wet sand on a rotating table in the greenhouse. The average diameter of each petiole, both at tip and base, was determined both before and after the experiments. Glass tubing, the diameter of which was slightly larger than that of the petioles, was split and used for encasing the latter to prevent bending. It was put in place while the plants were still small, about 7 to 10 cm. high, and was held in a vertical position by means of a burette clamp and a ring stand. A glass thistle tube, the lower end of which had been closed with sealing wax, was placed upright upon the apex of the petiole and was held in place by allowing it to slide freely within a slightly larger piece of glass tubing held in place by a second burette clamp. The thistle tube was counter-balanced by an equal weight attached to a fine wire thread running over a pulley wheel. This pulley wheel was that of a Sach's simple auxanometer which was used for determining the amount of elongation at intervals during the growing period (plate 31, fig. 1). Controls were carefully selected, one for each plant, and were similarly set up, except that no weight was added as described below for the treated plants.

TABLE I

Rates of elongation in inches per hour for five plants and their controls

PRESSURE IN GRAMS	PLANT 550 AND ITS CONTROL			PLANT 554 AND ITS CONTROL			PLANT 507 AND ITS CONTROL			PLANT 599 AND ITS CONTROL			PLANT 681 AND ITS CONTROL		
	Hrs.	Exposed plant	Control plant	Hrs.	Exposed plant	Control plant	Hrs.	Exposed plant	Control plant	Hrs.	Exposed plant	Control plant	Hrs.	Exposed plant	Control plant
25	16	.0413	.0413	16	.0337	.0550	16	.0218	.0303	16	.0116	.0313	16	.0012	.0103
50	12	.0450	.0616	12	.0466	.0858	12	.0366	.1083	12	.0666	.1158	12	.0083	.0241
75	12	.0460	.0916	12	——	——	12	.0575	.1083	12	.0516	.1000	12	.0025	.0316
100	12	.0208	.0333	12	——	.0625	12	.0225	.1041	12	.0591	.1040	37	.0011	.0424
125	12	.0166	.0460	12	——	.0583	12	.0175	.0700	12	.0175	.0566	25	.0008	.0120
150	12	.0000	.0141	12	.0058	.0316	12	.0008	.0608	12	.0108	.0650	70	.0009	.0079
175	12	.0016	.0208	12	——	.0358	12	.0191	——	12	.0250	.0775	48	.0008	.0058
200	12	.0000	.0150	12	.0391	.0326	12	.0050	.0166	36	.0130	.0194	72	.0003	.0016
225	12	.0066	.0258	36	.0016	.0305	36	.0042	.0112	12	.0050	.0166	24	.0008	.0013
250	24	.0038	.0154	84	.0027	.0112	14	.0041	.0100	24	.0058	.0100			
275	72	.0040	.0063				24	.0041	.0250	24	.0179	.0233			
300	36	.0025	.0091				24	.0012	.0083	24	.0020	.0108			
325							24	.0008	.0050	24	.0025	.0025			
350							24	.0004	.0029	24	.0008	.0054			
375							60	.0003	.0060	61	.0006	.0054			
400															

Either twenty-five or fifty grams of mercury were poured into the thistle tube of each plant treated. The needle of the auxanometer was then set at zero, and the plants were left to grow against this pressure. After 12 hours in some experiments and 24 hours in others, an equal amount of mercury was added. If the plant succeeded in raising this weight after a like interval of time, another 25 or 50 grams of mercury were added. If, how-

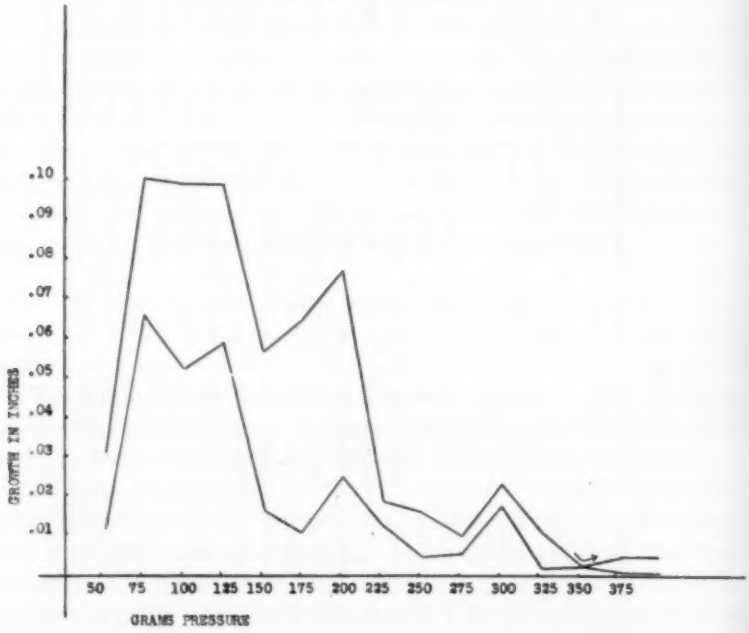

Fig. 1. Growth rates of plant No. 599 and its control represented graphically. Lower curve represents growth rate of exposed plant, upper curve rate of control plant.

ever, the petiole had not raised the weight, the mercury was not added; but the plant was left undisturbed until the auxanometer registered an increment of growth at the time of the periodic readings. Mercury was thus added until the plant could no longer raise the accumulated weight.

The data in table 1 show that the rate of vertical elongation of the petiole decreases with increase of longitudinal pressure, but not in exact proportion. From figure 1, which represents

graphically the growth rates of plant no. 599 and its control, it is seen that, in general, an acceleration of elongation of the control is accompanied by an acceleration of elongation of the exposed plant as well. Likewise, a retardation of elongation of either is accompanied by a retardation of elongation of the other, indicating that the plants are responding similarly to external conditions. It will be seen also that the first pressure of 50 grams made considerable difference in the rates of elongation. The curves are farther apart after a pressure of 75 grams is applied, and the distance between them remains large until the larger pressures of 225 grams to 350 grams are applied, when the decrease in rate of elongation of the exposed plant does not keep pace with that of the control. After 225 grams of pressure were added and until a pressure of 400 grams was reached, the rates of elongation are nearly the same, and at 350 grams of pressure the two plants are elongating at exactly the same rate per hour for a period of 24 hours. This seems to indicate that the first effect of pressure is to decrease the rate of elongation but that later the plant responds in some way to this stimulus causing an increase in the rate and that the total effect of the pressure is markedly to increase the strength of the plant and the greater the pressure the more the strength is increased.

The rates of elongation for all of the plants used were averaged for each respective pressure. The values of these rates per hour, where the 25 gram increments were used, are shown in table 2 and the corresponding graph in figure 2. As in the curves for the individual plants described above, here too we find that the effect of the increase of pressure becomes less in retarding the rate of elongation.

From the data in table 2 the amount of work done by the plants can be calculated. This can be done by substituting in the following formula: $W = 2.54\ g\ \Sigma\ (wd)$, where W = work in ergs, 2.54 = gram-centimeter equivalent, g = gravity constant or 980.6, Σ = sum of products of w by d, w = weight added at respective intervals, and d = distance respective weights are moved. For the whole group of plants where the pressure was increased by 25 gram increments, the average total work done per plant was found to be 569, 782.76 ergs; and where the pressure was increased by 50 gram increments, the average total work done per plant was 438,367.42 ergs. There was no ap-

TABLE 2

Average growth in inches per hour for respective 25 gram increments of pressure

PRESSURE IN GRAMS	EXPOSED PLANTS	CONTROL PLANTS
25	.0218	.0276
50	.0231	.0425
75	.0274	.0736
100	.0209	.0596
125	.0173	.0644
150	.0065	.0319
175	.0037	.0257
200	.0072	.0191
225	.0029	.0113
250	.0018	.0073
275	.0025	.0061
300	.0049	.0119
325	.0017	.0095
350	.0016	.0037
375	.0006	.0041
400	.0005	.0057

parent relation between the total work done and the total weight lifted. The maximum work done by any one plant was 1,498,175 ergs.

The greatest weight which the plant could lift under the conditions of the experiments varies from 175 grams to 500 grams, the average being 300 grams. The amount of the periodic increments does not alter the total load which the plant can lift.

Bending strength

After the plant was no longer able to raise the accumulated weight, its bending strength was determined. For this purpose the flectometer (fig. 3) was devised. This instrument consists of a dial (A) marked off in degrees, in front of which is mounted a pulley (B) with a pointer (C). A silk cord passed over the pulley and suspended two counterpoised vials (D and D′). Above vial (D) a capillary tube (E), bent in the form of a double curve, connected above through a stop-cock with a wider tube partly filled with mercury. A second silk cord attached to the same vial (D) passed up over the pulley (B) and thence horizontally for a distance of about one meter to the petiole (F). It is

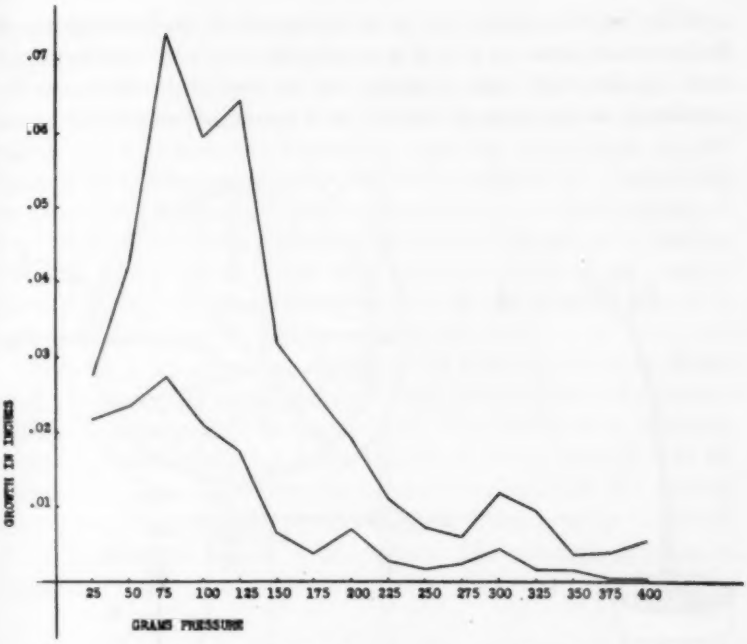

Fig. 2. Composite graph showing average growth per hour of all plants for periods of increasing pressures, based on data of table 2. Upper curve represents growth of control plants, lower curve the exposed plants.

attached to the petiole by means of a small wire hook. In order that the exposed and control plants might be tested in a comparable manner, the base of the petiole was held firm by a clamp attached at the same distance from the apex in the control as in the exposed plants, respectively. The pointer was set at zero and the stop-cock adjusted so that mercury dropped into the vial at the rate of 12 drops per minute. As the weight increased, the vial lowered, thus bending the petiole to an extent indicated by the pointer. The pointer was allowed to traverse the same angle for the exposed plant and its control. The angle chosen was a function of the length of the petiole. If the distance of the clamp from the apex was 19 cm., the angle traversed by the pointer was arbitrarily selected as 190°; if 15 cm., the angle selected was 150°; and so on. The weights of mercury required to bend the petioles to that angle were ascertained, thus measuring the bending strength.

Pennington (1910) used a scale mounted back of the tip of the inverted plant to which was attached a cord which passed over a pulley and bore a weight on its free end. He used the curvature of the stem as caused by a constant weight for meas-

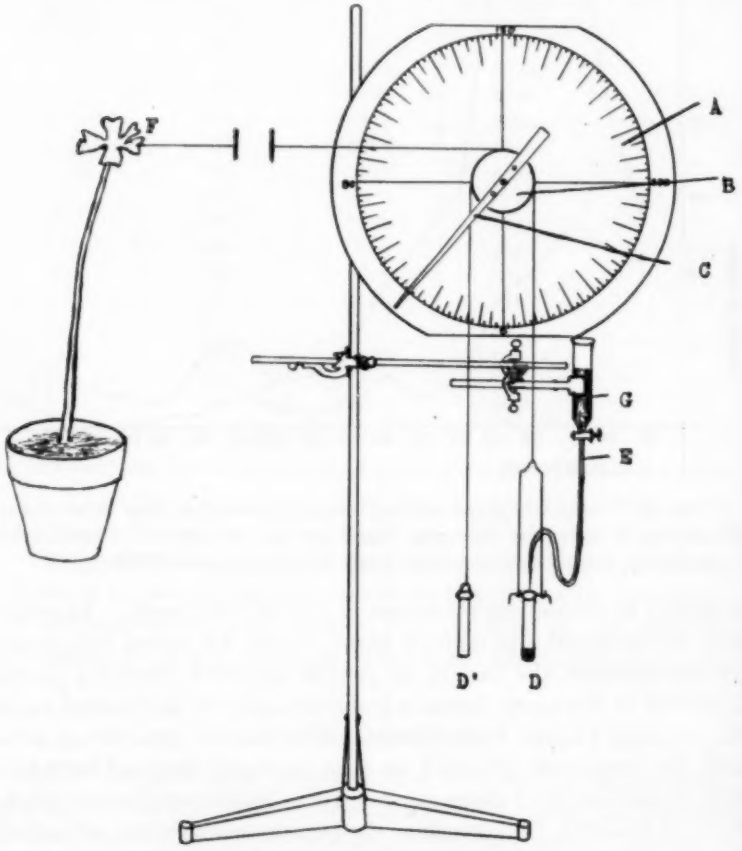

Fig. 3. Diagram of flectometer.

uring the resistance to bending. In our flectometer the weight is proportional to the length of the structure tested and is added very slowly, requiring all the way from twenty minutes to two hours. It furthermore seems that it is a better measure of the plant's bending strength to determine the weight required to bend it through a definite angle rather than to determine the

degree of bending by a certain weight added quickly. Plants vary greatly in their bending strength, and it is therefore unfair to apply a heavy weight to a weak plant or a light weight to a strong plant, as this may lead to considerable error in determining its real bending strength. Another advantage of the flectometer is that greater accuracy is attained by magnifying the movement with the pointer over the dial. A further feature of the flectometer is the comparatively long distance of the petiole from the pulley wheel. The very slight lowering of one end of the thread due to the bending of the petiole thus results in a negligible difference in the direction of the pull.

In table 3 are given the results of the bending strength determinations made on some plants exposed to longitudinal pressure and on their controls. In nearly every case the bending strength of the exposed petiole is greater than that of its control. In all except two cases, in which the bending strength of the control was greater than that of the exposed plant, the average diameter of the petiole was found to be larger. The average increase in strength for the plants investigated in this way was found to

TABLE 3

Bending strength of some petioles as determined by flectometer

PLANT NO.	EXPOSED PLANT				CONTROL PLANT		
	Length	Average diam.	Weight carried	Flectometer readings	Length	Average diam.	Flectometer readings
	cm.	*mm.*	*grams*	*grams*	*cm.*	*mm.*	*grams*
287	13.8	4.48	350	25.5629	17.5	4.84	30.0403
303	13.5	4.955	350	36.6566	13.5	5.10	33.3487
502	14.0	4.255	250	21.8802	14.6	3.81	16.3187
564	18.4	4.79	350	31.0081	19.9	3.585	17.3841
566	22.2	5.535	350	39.8913	23.7	5.57	31.0613
568	19.0	5.18	350	35.2213	17.0	4.44	15.7679
570	16.4	5.18	400	14.2509	25.0	4.07	14.6615
550	20.2	5.18	300	24.5395	24.5	3.45	13.8050
553	17.5	4.14	225	22.7851	22.0	4.025	15.5787
554	18.5	4.945	250	28.3726	25.0	4.0	14.2610
555	17.7	4.55	225	19.2204	28.3	5.245	29.9279
677	20.0	4.94	300	23.2325	19.5	4.28	21.6967
679	13.17	4.42	275	25.5953	22.5	4.29	32.9545
681	11.0	4.84	275	36.8603	17.0	4.18	16.9260
683	15.0	4.74	300	36.8185	14.0	5.37	37.2496
715	23.7	4.81	300	13.4910	28.4	4.78	10.2437
720	21.5	5.81	300	23.0787	16.8	5.56	22.3337

be 18 per cent. The average bending strength in terms of grams for the exposed plants was 26.9685 and for the controls it was 21.9740.

That this increase in bending strength is a permanent condition was shown by first determining it for a number of plants immediately after release from the pressure and again after the plants were left in the dark room for four days. The results were the same. If the resistance to bending had been the result only of turgidity, it seems that a decrease in turgor would follow release from the pressure and thus decrease in the bending strength.

Structural effects of longitudinal compression

The experiments described above show that longitudinal pressure during growth retards the rate of elongation and increases the bending strength of the petiole of *Podophyllum*. There seems to be, also, a certain structural modification resulting from longitudinal pressure. In this petiole there is an outer ring of bundles bounding a central pith and lying next to the inner margin of the cortex. Other bundles of the nature of leaf traces are distributed within the pith. Bordering the phloem of each bundle toward the exterior are thick-walled cells. Sections of the petiole of a control plant show very little of this mechanical tissue, whereas in sections of the petiole which grew against a final maximum pressure of 400 grams it is well developed. Furthermore, the walls of the parenchyma cells between the bundles also become thickened, and the cells are transformed into stereome. This difference is very evident in the sections of individual bundles highly magnified and shown in figures 1, 2, and 3 of plate 30. There also seems to be some difference in the organization of the xylem and in the character of the walls of the vessels.

EFFECTS OF FLEXATION

Some of the work on the effect of pressure and tension upon growth has been done by others with the view to explaining the eccentric growth of stems of Coniferous trees and the presence of "redwood." The trunks and branches of many trees have more wood on one side, and the annual rings on this thicker side are often reddish in color, resembling heartwood, the walls of the cells being much thicker and the wood much harder.

Burns (1920) exposed seedlings of pine to a bending motion to determine whether or not wind action could be the cause for the production of this mechanical tissue. He says that no "redwood" was formed nor did any eccentric growth take place as result of this bending. Koehler (1919), on the contrary, tied saplings in a circle and got red heart-wood on the inside. He attributes the formation of this "redwood" in this location to compression and not to a gravitation stimulus. Miss Gilchrist (1908), working mainly with sunflowers, reports that plants so swayed in one plane "are shorter and thicker" than control plants, that the "diameter in the plane of swaying is greater than that at right angles," that the "xylem in the plane of swaying is greater than in the transverse plane," that "a greater amount of xylem is produced than in stems of controls," that "the rigidity is greater in the diameter in the plane of swaying than in transverse diameter," and that "swaying 'in the wind' produces greater eccentricity." Hartig (1896), observing the effect of wind on trees, believed that longitudinal pressure on the cambium caused the production of "redwood." Later, however, (1901) he concluded that gravity may also act as the stimulus. Cieslar (1896) attributed the formation of "redwood" to a pressure stimulus as a result of bending young spruce trees. Ursprung (1901) maintained that it was a compression-strain stimulus resulting from the weight of the structure and the action of wind that caused the distribution of radial growth. Kny (1882) accounted for this one-sided increase in the growth of tree trunks on the basis of one-sided leafing of the tree causing one side to be heavier than the other. Growth is thus inversely proportional to the external pressure exerted upon the growing cells. Wiesner (1892) also attributed eccentric growth to unequal size and distribution of the leaves. DeVries (1876), by winding twine around stems, concluded that the presence of annual rings results from greater bark pressure at some seasons of the year than at other seasons. Krabbe (1884), however, proved that the bark pressure is never great enough to retard growth. Wortmann (1887) found that the collenchyma of the cortex of bandaged plants became greatly thickened. He attributed this to the fact that these cells could not reach their normal surface tension. Detlefsen (1882) also attributed eccentricity to bark pressure. Newcombe (1895) concluded that

the formation of mechanical tissue is not always caused by mechanical forces but calls the responses self-regulatory phenomena. Keller (1896), in considering the strengthening of the fruit-bearing axis, held that it is not due to tension because of the weight of the fruit nor because of the fruit-bearing itself, but that it is the change in direction of the axis which causes the anatomical changes. Pieters (1896), on the other hand, found that lignification of cell walls and increase in cells go hand in hand with fruit development. Vöchting (1902) found no increase in mechanical tissue in weighted sunflowers, some of which had been decapitated. In Savoy cabbages, all of which were decapitated, he found only a slight increase in mechanical tissue, but this was not proportional to the weights used. By removing the flower buds, he greatly retarded the formation of mechanical tissue in these plants. Subsequent addition of weights did not cause the mechanical elements to reappear. But when he grafted another stem onto the decapitated one, the mechanical tissue again began to form, although this additional weight was much less than the weights which he fastened to the decapitated stem.

In my experiments with *Podophyllum* petioles a device called the flector was constructed for bending the petioles back and forth in one plane. This consisted of a bicycle wheel driven by a small electric motor. To the wheel was eccentrically attached a stiff wire about five feet long, which was made adjustable on the wheel so as to increase or decrease at will the amplitude of the bending. This wire was held horizontal and at any desired elevation above the table by having it pass over adjustable wheels. The tips of the petioles were fastened along the side of the wire by cord so that they would be pulled first in one direction and then in the opposite. To avoid injury to the petioles, the cord was looped about a rubber band cut from tubing, slit open, and placed about the petiole just beneath the peltate blade.

Thirty-one plants were set up in this manner when they were about three or four inches tall, the extent of bending being only about two inches. The amplitude of bending was increased from two inches to about eight inches during the period of growth which lasted for a week to ten days. As soon as the petioles reached their maximum elongation, their bending strength in

two planes was determined by means of the flectometer, one plane being the same as that of the bending by the flector and

TABLE 4

Bending strength of plants which were flexed back and forth, and of controls for some of them

BENDING STRENGTH IN PLANE OF FLEXATION	BENDING STRENGTH AT RIGHT ANGLES TO PLANE OF FLEXATION	PERCENTAGE INCREASE	BENDING STRENGTH OF CONTROL PLANTS
grams	*grams*		*grams*
13.4177	14.5611	7.8	
24.4600	25.1233	2.6	
18.2003	18.9775	4.0	
16.0513	18.7273	14.0	
36.2526	38.0660	4.7	
15.9204	19.8324	19.7	
16.6287	16.9017	1.5	
28.4787	32.6488	12.7	
13.6571	14.7405	7.3	
17.6905	19.5478	9.5	
31.3711	37.1264	18.0	
14.8031	14.7245	.5	
34.1945	34.7887	1.7	
15.9371	19.9948	20.0	
11.9029	15.1808	21.0	
9.9481	10.1181	1.6	
16.4048	18.8279	12.8	
23.9100	28.9750	17.0	
14.9889	18.1944	17.0	
13.7554	15.4380	10.8	
10.0909	11.7310	14.0	
15.6587	18.4587	15.0	
8.0054	9.3630	14.5	
20.9037	28.6600	27.0	15.3924
16.8190	24.3812	31.0	21.7313
9.7771	18.2596	46.0	17.5165
30.7186	34.7196	12.0	18.3255
14.7183	16.7846	12.0	18.3094
22.0045	27.6760	20.0	20.1090
30.8175	38.7051	20.0	21.1216
19.4123	24.4924	20.0	14.6061
Average 20.4194	23.3523	14.0	18.3889

Increase over controls (based only on plants where controls were used): in plane of flexation, 12 per cent; at right angles to plane of flexation, 40 per cent.

the other at right angles to it. In table 4 is given the bending strength of these plants together with the bending strength of some of their controls. The bending strength of these plants, when determined for the same direction as the plane of flexation, was found to increase 12 per cent over that of the controls; but in the direction at right angles to this plane of flexation the increase was 40 per cent. This shows that, in *Podophyllum* at least, flexing motion results in an increase of bending strength. In all cases, except one, the bending strength at right angles to the plane of flexation was found to be greater than that in the plane of flexation. The maximum difference was 46 per cent and the average was 14 per cent.

The effect of flexation upon the bending strength of the plant is here seen to be approximately the same as that of longitudinal pressure. Here, however, the increase in the resistance to bending may be the result of the production of mechanical tissue or of a modification of form of the petiole. The length in mm. of the maximum diameters in the two planes was determined for ten plants as follows:

Same plane:	4.90	5.64	5.40	6.60	6.00	4.84	4.92	4.80	5.43	4.53
Right angles:	4.94	6.48	5.34	6.60	6.34	4.97	5.35	5.25	5.82	4.84

This gives an average maximum diameter in the same plane as flexation of 5.306 mm. and an average maximum diameter at right angles to the former plane of 5.5593 mm., showing a difference of .287 mm. This result of flexation in producing a difference in the diameter of the petiole may account for the difference in bending strength, although this evidence cannot be considered as being conclusive.

MEASUREMENT OF THE ENERGY OF GEOTROPISM

The force exerted by a petiole of *Podophyllum* in elongating vertically has been measured above. The force required to bend the petiole has also been ascertained. It now remains to be determined whether a stem or petiole in curving is capable of exerting more force than that which is just required to bend it. This can be done by finding the lifting power of such an organ during geotropic curvature.

Many workers have attributed geotropic curvature to the effects of pressure and tension upon growth. Ricome (1920),

supports the theory that negative geotropism may be due to the weight of the terminal portion of the plant causing a compression below which stimulates growth and a tension above which retards it. This pressure may not be due to the weight of the tissues, but it may be an increased osmotic pressure, as suggested by DeVries (1880). He concluded that gravity produces an increased osmotically active material in the cells of the lower side. Cielsielski (1872) observed a difference of the sap on the opposite sides; the cells of the convex-becoming side contained a thin watery protoplasm, and the cells on the side becoming concave had a denser and more opaque plasma. Kohl (1894) found in the sporangiophores of *Phycomyces* that in geotropic stimulation the plasma of the concave side became much thicker and that of the convex side thin and watery. On the other hand, Hilburg (1881) found that osmotic pressure of the concave side of leaf joints and stem nodes of various plants is greater than that of the convex side. Wortmann (1889) did not think that osmotic pressure had anything to do with geotropic curvature, since he could find no difference on the two sides. He thought that the thickened plasma on the concave side thickens the cell membranes on that side, making them less elastic than those of the convex side. Copeland (1900) found no difference in osmotic pressure on the two sides of stems split lengthwise and stimulated geotropically four days. Kersten (1907), using the plasmolysis method, also was unable to find any change in the osmotic pressure on the two sides. Miss Schley (1920) found that the osmotic pressure is greater on the convex side during the geotropic response, rising during stimulation and reaching a maximum at or before visible response, and decreasing as the response nears completion.

Czapek (1902) explained the response on the basis of chemical changes affected by the geotropic stimulus. Kraus (1879–1884) observed a rise in the percentage of reducing sugars and a diminution of acidity, especially in the under surface of a shoot placed horizontal. Any chemical change leading to a change of osmotic pressure would give similar results. A further evidence that a chemical change takes place is afforded by the observations of Chapman, Cook, and Thompson (1924), who found that with a concentration of CO_2 above 40–45 per cent growth ceases and with it all responses to gravity.

Haberlandt (1900) and Němec (1902) both attributed geotropic response to the settling of bodies in the plasma in a manner similar to the otoliths of animals. Zaepffel (1921) made a detailed experimental study of geotropism in the various parts of seedlings of certain grasses and concludes that movement of the starch grains disturbs the equilibrium between starch grains and the products of their hydrolysis, giving a difference of osmotic pressure which causes unequal growth of upper and lower parts of the cell. Němec (1902), Zollikofer (1918), and others found that in certain plants statolith starch disappears when placed in the dark and with the disappearance of the statolith starch also goes the ability to respond to the stimulus of gravity. Small (1920) and Bose (1920, 1921) assumed that the particles which settle carry electrical charges thus setting up a difference in potential within the cells. This increases the permeability to ions and conductivity in the upper side of the petiole more than in the under side. It also gives greater relative turgor on the under side, greater growth and therefore curvature upwards. They have been opposed in their theory by Blackman (1921) and Snow (1921) and also by Cholodny (1923). Blackman and Snow contend that an electrical potential great enough to produce the results which Small and Bose assume could not result in this way. Cholodny admits only the assumption of Small that electrically laden particles settle to the bottom of the cell.

For my experiments an instrument was constructed which automatically dropped a small weight into a container attached to the tip of the petiole, every time it raised the distance of a millimeter or less, thus pulling it back to its original position, that is, keeping the plant continuously horizontal. A kymograph records the time when each weight is dropped. This instrument may be called a tropograph.

The plant (fig. 4) was placed horizontal; the petiole encased in split glass tubing which was clamped firmly in position. Attached by a fine wire hook inserted in a loop of braid over the end of the petiole, a silk thread suspended a glass vial (B). This vial was counterbalanced by another (B′) over pulley D. In order to make certain that the braid did not slip away from the tip of the petiole, a short piece of thread was passed back of the braid just beneath the petiole, out through the deep clefts of the leaf and tied at the outside. Thus, when the plant was in

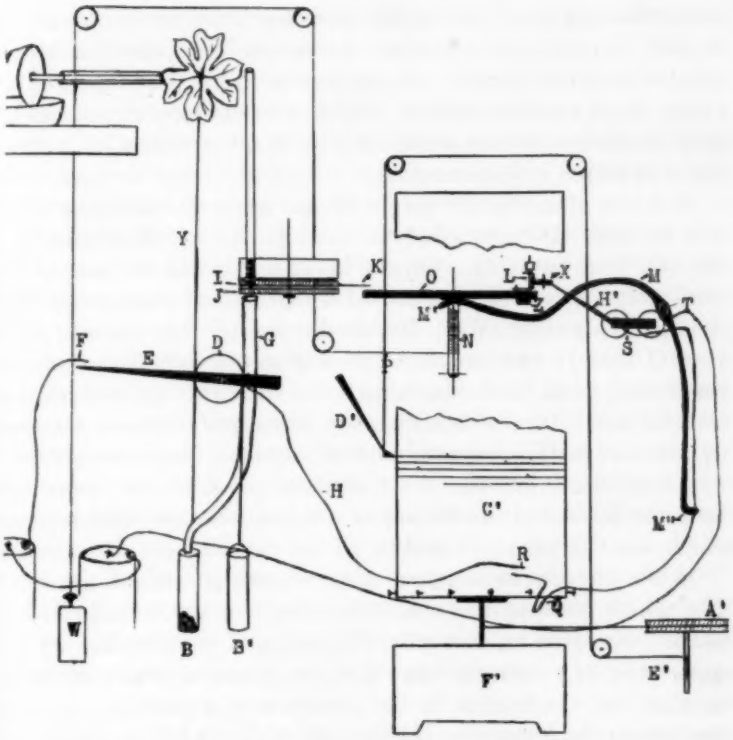

Fig. 4. Diagram of tropograph.

position, practically no weight was sustained by the petiole itself except the fine silk thread and the braid. The weight of the petiole was borne by the glass tube. Above the pointed end of arm (E) a copper wire was located connecting with four dry batteries in series. From its broader end a second wire connected with an electro-magnet (S) which operated a shot-dropping device; this magnet in turn was connected with the batteries. When the plant was placed in position, the pointed end of the arm was only 1 mm. or less from the wire (F). As the petiole rises, its movement is magnified five times at the tip of the arm. Only a very slight movement of the petiole therefore causes the circuit to close at (F) and by a mechanism, described below, a steel shot 4.5 mm. in diameter and weighing .3471 gram dropped through the tube (G) into the vial (B). In most

cases the weight of this single shot was sufficient to break the circuit. After a short period the petiole rose again and once more closed the circuit, causing another shot to drop into the vial. By a continuation of this process the petiole was kept from bending upwards while for a time it continued to increase the load which it was carrying.

For the dropping device an electro-magnet was mounted so that its arm (H′) extended to a catch (X) which prevented a disc (O) from rotating. On the lower portion of the axis of this turn-table (N) was wound a cord which passed over pulleys and suspended a weight (W). Beside the disc (O) two circular brass discs (I and J) were mounted closely one above the other, the lower one fixed, and the upper one movable on the central vertical axis. Over a hole through the upper disc was attached a glass tube containing a column of shots the lower one of which rested on the lower disc. At another place in the lower disc the same distance from its center was a similar aperture beneath which was the tube (G) leading to the vial (B).

When the electro-magnet was charged, it opened the catch (X), which allowed the disc (O) pulled by the weight (W) to rotate. An arm on this disc (O) engaged a lever (K) on the upper disc (I), causing that disc to rotate a short distance, carrying the single shot in the aperture to a position over the aperture in the lower disc (J) through which it fell into tube (G) and thence to the vial. A spring drew the lever (K) back to its former position allowing another shot to fall into the hole of the upper disc. The disc (O) was prevented from rotating again by the catch (X), which was not released until the electro-magnet was again charged. This could not happen for at least one minute, due to a second break in the circuit (R). At this point was placed a kymograph bearing a row of pegs at the base of the drum. As the drum revolved the pegs moved below the wire (Q) and raised it sufficiently to make contact again. These pegs were so spaced as to make contact at one-minute intervals, thus allowing the plant to return to equilibrium after each shot was dropped. A heavy wire (M) was so mounted near the electro-magnet that a projection (Z) on the underside of the turn-table (O) struck the end of the wire, thus breaking the second contact. Near the kymograph was placed a pulley (A′) turned by means of a belt connected with the shaft of the kymograph.

To the axis of the pulley was attached a fine silk thread which wrapped around it. This thread suspended a stylus (D′) which drew a spiral line on the kymograph, as it steadily raised by the thread wrapping around the pulley. When a contact was made, the arm (H′) of the electro-magnet was moved and the stylus was caused to move vertically, making a jog in the spiral line and thus indicating when the shot was dropped.

At first some difficulty was encountered when some of the petioles underwent torsion. When this occurred, the petiole would bend toward the right or left, depending on the direction of the torsion. This was overcome by mounting two small pulleys, one on either side of the tip of the petiole. A silk thread was attached to the braid over the petiole and passed over the two pulleys and downward past two other pulleys mounted close together and then attached to the vial. Thus it made no difference if the pull of the petiole were lateral or vertical; the circuit would be closed just the same, resulting in the shot being dropped into the vial.

From the kymograph records the number of shots dropped per hour was calculated and checked with the number of shots in the vial at the end of the experiment. The shots dropped in successive hours were for six plants as follows:

												Total
1:	17	6	6	14	11	9	7	1	—	—	—	71
2:	34	11	6	12	17	12	6	—	—	—	—	98
3:	16	9	9	9	11	14	14	10	8	—	—	92
4:	9	5	7	6	10	10	6	—	—	—	—	53
5:	3	2	1	5	3	4	4	4	4	4	3	37
6:	23	9	14	13	10	5	6	4	4	4	—	92

The reaction time was found to vary from 24 minutes to 88 minutes, with an average of 57 minutes. It was also found that the maximum load which the plant can lift in this manner ranges from 11.451 grams to 66.553 grams, with an average of 32.804 grams.

It is seen from these data that in nearly every case the number of shots dropped during the first hour is relatively large. There is a decrease in the number of shots dropped during the next hour, this decrease being larger in some cases and smaller in others. During the third hour the number of shots dropped may increase, or this increase may not take place until the third,

fourth, or fifth hour. But in every case there is a second maximum following the first maximum of the first hour. In several cases there was a third maximum.

In figure 5 are plotted the smooth curves for the total load at the end of each hour for four of the plants. In this figure the first part of the curve is convex rising rapidly. This represents the large number of shots dropped during the first hour. During the second hour the increase in the load slows up a bit. This

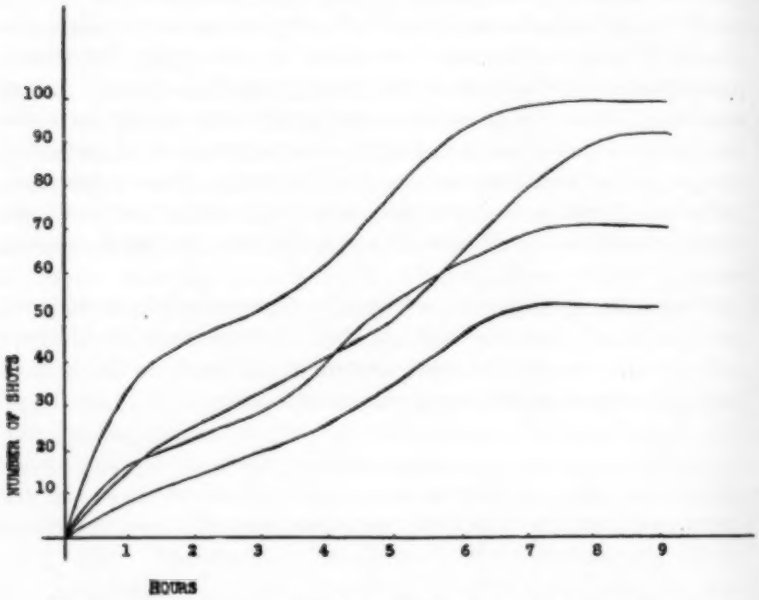

Fig. 5. Smooth curves showing number of shots in vials at successive hours for four plants.

gives a concave curve following the first convex portion. This is followed by a convex curve again indicating the second increase in load. As the number of shots dropped per hour decreases, the curve gradually flattens out until the plant has attained its maximum pulling power. This type of curve was produced in most of the thirty experiments which were performed with the tropograph.

If the weight and the glass tubing be removed from one of these petioles, the petiole immediately bends to the upper side

at a visible rate (plate 31, fig. 4). The force bending the petiole to one side is often sufficient to bring the distal end in contact with the soil (plate 30, fig. 4). In one case the epidermis and cortex were ruptured because of the curvature. If it be first placed erect, the same curvature will occur, but later the terminal portion of the petiole bends upward in response to gravity.

A variation of the turgidity of the cells on the two sides of the petiole doubtless plays an important part in this curvature. That curvature of the petiole of *Podophyllum* may result from a variation of turgor was shown by removing one leaf from fertile shoots. Within less than an hour each shoot had bent over in the direction of the exposed cut surface where the leaf had been removed. The loss of water from the cut surface had decreased the turgidity of the cells on that side sufficiently to bend the distal portion of the shoot to nearly a right angle in some cases. A further indication that osmotic pressure plays an important part in such curvature of stems was obtained by taking a plant after it had curved upon release from the tropograph, peeling off the epidermis from the convex surface, and inverting the petiole in a 10 per cent salt solution. After about an hour the petiole had become straight. When rinsed and placed in fresh water, it again became curved as before. In both of these cases the curvature was brought about by contraction of the one side rather than by an elongation of the opposite side. This would seem to disprove the contention noted in the literature above that geotropic curvature is due to the extension of the lower side, and shows that it is due to a contraction of the upper side.

DISCUSSION

Pressure is known to exert a pronounced influence upon certain phases of growth and upon certain plant reactions, and it has been suggested as a possible cause of other cellular processes. Cell elongation has been shown by Newcomb (1894) to be altered by pressure. Roots encased in casts of plaster of Paris were found to have mature cells much smaller in size than normal cells and with thin walls. Likewise, cell differentiation is altered by pressure, as Pfeffer found in the Windsor bean, where spiral tracheae had developed near the tip of the root, normally developing much farther back. Jeffs (1925), in his study of root-hair formation, regarded pressure as the important factor,

resulting from cellular interaction, in the production of root-hairs. He found that as the sub-epidermal cells of the root ceased elongating, thus checking vertical elongation in the epidermis, lateral evaginations of the epidermal cells due to lateral pressure developed into root-hairs. Farr (1916), in the study of cell-division of the pollen-mother-cells of certain dicotyledons, interpreted quadripartition by furrowing as being influenced by the spherical form of the mother-cells and their loose arrangement in the pollen chamber, the mother-cells thereby being free to undergo such change in volume and form as their internal constitution would favor. In most typical plant cells a cellulose wall opposes change in form and resists increase in volume; hence pressure of the cell content against the wall may account for the formation of the cell-plate.

The present study of the petiole of *Podophyllum* has determined the composite effect of pressure on all of the processes involved in growth and contributes to our knowledge of the physiology of growth by showing the influence of pressure on its rate as well as the energy relations involved both in growth and in tropic responses. It also suggests a means for the investigation of other growth movements which result from stimuli of light, wounding, etc. It gives further light on our knowledge of cellular interaction in the production of mechanical tissue as indicated by increase of strength, and aids in interpreting the responses of plants to movements effected by such agencies as wind and gravity.

It usually has been assumed that pressure decreases the rate of growth. While this is in a sense true, it does not constitute an exact description of the situation. Growth rate might be an inverse function of pressure; yet it is not necessarily proportional to it. The first effect of pressure in all of these experiments was found to be a retardation of growth, and if the weight is not further increased the normal growth rate is resumed. This is seen from the daily records where the first reading following the addition of weight is usually less than subsequent readings until addition of more weight. Thus the first effect of retardation is followed by a stimulation of growth. This is what Hegler (1893) found in the case of tension. At first it might seem that the rate of growth is inversely proportional to the weight, for the curves representing the growth of the plants and

their controls gradually separate. But the fact that this does not continue and that the rate of growth of the plant exposed to pressure may exceed that of the control shows a later stimulating effect of the pressure.

The maximum energy which the petiole of *Podophyllum* with an average diameter of 4.2 mm. at its tip exerts in growth against pressure is that sufficient to sustain a weight of 550 grams. This would be equivalent to 38.75 grams per sq. mm. or a maximum of 3.75 atmospheres. The greatest pressure developed by these petioles is thus less than any of the pressures which Pfeffer found to be developed by roots of *Vicia faba*, which ranged from 5.15 to 19.35 atmospheres. The need for a pushing force by the root greater than that of a stem is obvious from the simple fact that the root must be able to force itself into the soil.

The ability of the petiole to lift a greater load after it had raised a certain weight shows that it increases in strength and points to the probability that additional mechanical tissue is produced. Further evidence of this is to be found in the average increase of 18 per cent in the bending strength of the petioles grown against pressure. These results are not in harmony with those which Pennington (1910) obtained. He found no increase in the bending strength of plants which he subjected to longitudinal pressure, nor could he find any increase of mechanical tissues when studied microscopically. This dissimilarity of results may be due to the use of different plants with apical meristem and to the different methods employed.

That pressure increases the bending strength was also shown in the flexation experiments. In flexation there is produced alternate compression and tension of the tissues on the two sides of the petiole in the plane of flexation. Here the increase in bending strength is about 26 per cent. This is comparable to the average increase resulting from longitudinal compression. Miss Gilchrist (1908), working in a similar manner with sunflowers, likewise found that flexation increased the strength of stems. One important difference is noticed, however. The sunflower stems became stronger in the plane of flexation than at right angles to it, while in *Podophyllum* the strength of the petiole at right angles to the plane of flexation was found to be the greater. In my experiments the difference in the bending strength in the two planes varied all the way from .5 per cent in favor

of the plane of flexation to 46 per cent in favor of the plane at right angles to that of flexation with an average increase of 14 per cent. Miss Gilchrist also found that the diameter was greater in the plane of flexation than in the plane at right angles to it. In my experiments with *Podophyllum* it seems that the diameter of the plane at right angles to that of flexation is larger, which might, in part at least, account for the difference in bending strength in the two directions. Just how this result is produced by the action of bending, it is difficult to say. It may be that the alternate compression and tension permits less deposition of wall material in certain places.

The results of flexation are not necessarily the same as those which might follow the action of wind. Much of the work by others has been more or less confusing for the reason that what have been called wind effects have been merely bending effects. The two may be very different, for the action of wind involves increase in transpiration, which in turn would alter other internal processes that are not affected in such experiments as were performed by Burns (1920), and Gilchrist (1908). Cavara (1912), on the other hand, found that the excessive transpiration accompanying wind resulted in the shortening of the stem and tended to produce the rosette habit. In my experiments the bending did not seem to alter the average length of the petiole; the effect was purely mechanical.

That turgor plays an important part in the raising of the weights of the first group of experiments is doubtless true, but it is doubtful that it is responsible for the increase in strength as determined by the flectometer. If the weight does increase the turgidity of the petiole, then conversely, when the weight is removed, the turgidity should decrease to the normal. It is furthermore not likely that bending back and forth has a pronounced effect upon the turgidity of the tissues. If there were no structural changes produced, there would doubtless not have been such consistent differences in the bending strength in the two directions at right angles to each other as were obtained in these flexation experiments. On the other hand, the bending strength should have been approximately the same in the two directions if turgidity alone accounts for the increase. The structural basis of this increase of strength is further borne out by the microscopic sections of bundles. Ursprung and Blum (1924)

account for all enlargement as a consequence of wall extension and not increased turgor pressure.

The effect of compression in producing increase in strength in the petiole of *Podophyllum* and the production of mechanical tissue supports the contentions of Hartig (1896), Ursprung (1901), and Koehler (1919) as to the formation of "redwood" in conifers, since they attribute the presence of this tissue to an increased compression stimulus on the one side of the stem.

As stated above, Ricome (1920) attributed the geotropic curvature of a stem to compression and tension stimuli. The pressure on the lower side of the horizontal plant acts as a stimulus increasing growth and the tension on the top side decreasing it. If the stem is to curve upward, according to Ricome, as a result of an increase in growth below and a decrease above, then the difference not only must represent a force equal to the weight of the stem which gives rise to the altered growth rates but also must represent an additional force equal to that necessary to bend the petiole. This theory does not coincide with Hegler's (1893) observations on the effect of tension on growth, nor with mine on the effect of pressure. Tension and pressure both seem to retard growth at first. Furthermore, the rupturing of the petiole on the side which was beneath when horizontal indicates that negative geotropism is the result of a contraction of the upper side. This is also borne out by my experiments with the fertile shoots from which one leaf had been removed and with the petiole which was placed in the salt solution.

The weight which the petiole of *Podophyllum* will lift in response to the stimulus of gravity was found to vary from 11.451 to 69.43 grams, with an average of 32.804 grams. To arrive at the total energy of the petiole in our tropograph experiments, we must consider, in addition to the weight which it is sustaining while horizontal, the force which would be required to bend the petiole at right angles. As the petiole is sustaining a maximum weight of 69.43 grams, it has remained straight and still contains potential energy equal to that necessary to bend it. Therefore the total energy of the petiole is equal to the weight sustained plus that required to bend it. From the flectometer records it is estimated that an average weight of 30 grams would be necessary to bring about the bending. Adding this to 69.43 grams would give a total of 99.43 grams as the total energy of the horizontal petiole.

That the force continues to increase for a period of time, as long as 30 hours in some cases, is significant. Schley (1920) found that the osmotic pressure continued to increase until curvature began and then decreased until curvature ceased. It is difficult to understand why this should occur. In the light of my bending-strength determinations, to the effect that the more the petiole is bent the more the force necessary to continue the bending, it would seem that in geotropic curvature, if the force responsible for it is osmotic pressure, then the latter must continue to increase until the petiole is erect and the osmotic pressures of the two sides again become equalized. The tropograph records indicate that whatever the source of the force producing geotropic curvature it increases long after the response begins. In any theory of geotropism this must be taken into account. Not only this but also the manner in which the force increases must be explained. The tropograph records have shown this increase to be periodic, first a rapid increase followed by a less rapid increase, and then a second rapid increase followed by another less rapid rise until the maximum force is developed. In some cases a third increase was found to occur.

These findings are not in accord with the observations of Zollikofer (1918) that the geotropic sensitivity is lost in the dark. If statolith starch disappears in the dark and the responsiveness to the geotropic stimulus decreases, then I am at a loss to explain the continued rise in the force developed in my experiments, for they were performed in total darkness, except for a dim red light when the readings were taken.

If we adopt Němec's theory of geotropism and assume that it is the result of the settling to the bottom of particles within the protoplasm, we can conceive of an increase in this force as taking place with the unequal settling of these particles. The heavier particles will settle first and by their hydrolysis perhaps increase the osmotic pressure below and decrease it above giving the first rise in our curve. Somewhat smaller particles will settle more slowly and while causing the force to continue to increase will probably not cause it to increase at the same rate, accounting for the first concave portion of our curve. The question now arises as to how to account for the second rise and in some cases for the third rise. If it is assumed that the particles are of two or three general sizes or that there is a synthesis

of new particles, the unequal settling of them would give a periodic increase of this force. It seems that even in Small and Rea's theory (1920) of a variable permeability resulting from the differences in potential which follow a "creaming effect" that we must assume that the particles are of several sizes or newly synthesized, thus giving a periodic permeability.

These experiments were conducted in the Plant Physiological Laboratories of the State University of Iowa, and I am greatly indebted to Dr. C. H. Farr for his many helpful suggestions in the prosecution of the work.

SUMMARY

1. The maximum mechanical energy which a plant is capable of expending during growth may be measured by determining the maximum weight which the plant can lift when erect or the force exerted in lifting a weight when horizontal, plus that required to overcome its own rigidity in bending.

2. The maximum weight which a petiole of *Podophyllum* will lift when erect varies from 175 to 500 grams, with an average of 300 grams.

3. The maximum weight which a petiole of *Podophyllum* will lift when horizontal varies from 11.451 to 69.43 grams, with an average of 32.804 grams.

4. The force required to bend the petiole of *Podophyllum* varies from 9.777 to 39.891 grams, with an average of 26.16 grams. For these measurements the number of degrees of the angle of bending of each petiole was ten times the length of the petiole in centimeters.

5. Longitudinal pressure on the apex of an erect petiole results in an increase in the ability of the petiole to overcome such pressure. To lift the maximum weight so applied 10 days are required, during which the weight has been increased by 50 grams daily.

6. Lateral pressure or weight applied to a horizontal petiole of *Podophyllum* increases the ability of the petiole to curve geotropically, overcoming such pressure or weight. To lift the maximum weight so applied, from 6 to 29 hours are required during which the weight has been increased most at first, 13.537 grams per hour, with a second maximum, about 4.5 grams per hour, after about 4 hours. The rate of addition of weight falls

to 2.777 grams per hour after the first maximum and to zero after the second.

7. Pressure on the apex of a petiole of *Podophyllum* results in an average increase of 18 per cent in its rigidity.

8. Flexation—that is, the alternate bending back and forth of a stem-like axis—increases the rigidity of the structure flexed. This increase is less in the plane of flexation, being 12 per cent, than it is in the plane at right angles, in which the increase is 40 per cent.

9. The maximum work which a petiole of *Podophyllum* can do during growth is 1,489,195 ergs in 13 days.

10. In making these determinations the apparatus used consisted of: (a) Sach's auxanometer for measuring growth under longitudinal compression experiments. (b) A flector for accomplishing flexation at a constant rate over a period of several days. (c) A flectometer for measuring the rigidity of a stem, root, peduncle, hypocotyl, or petiole. (d) A tropograph for measuring the maximum force which a stem, hypocotyl, root, peduncle or petiole is capable of exerting during tropic curvature, and the rate of increase of this tropic force if curvature is prevented. The last three pieces of apparatus named were devised especially for this study.

MACALESTER COLLEGE,
ST. PAUL, MINNESOTA.

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Explanation of plates

PLATE 30

Fig. 1. Single bundle of plant grown against pressure.

Fig. 2. Single bundle of control plant.

Fig. 3. Another bundle from same plant as in fig. 1.

Fig. 4. Petiole as bent immediately upon release from tropograph and removal of glass tubing.

PLATE 31

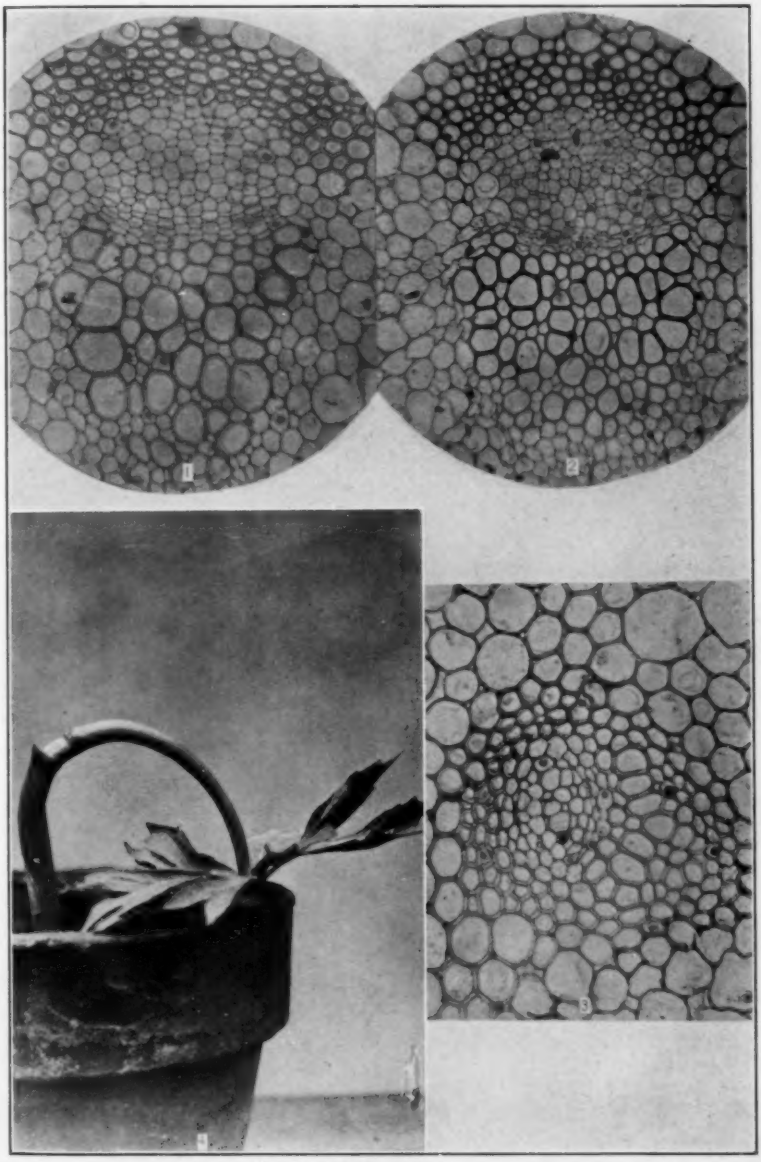
Fig. 1. Plant shown growing against pressure.

Fig. 2. Same petiole as of plate 30, fig. 4, several days later.

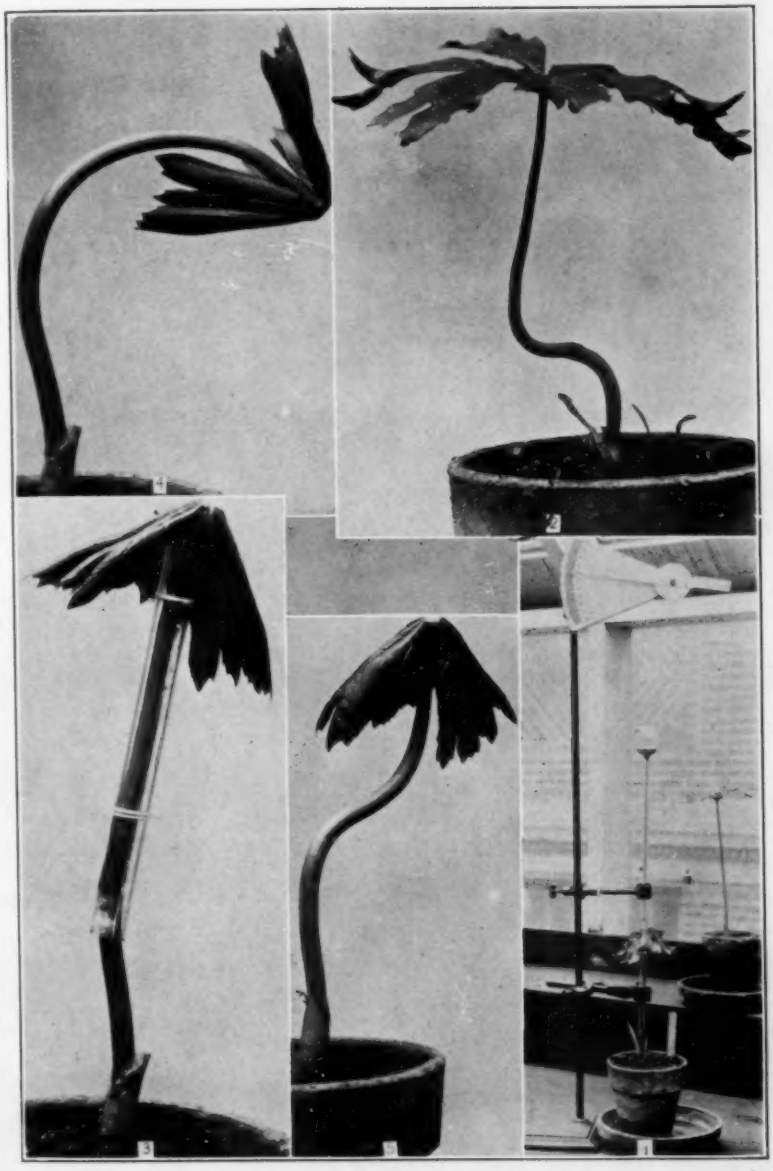
Fig. 3. Another petiole just taken from tropograph and before removing glass tubing.

Fig. 4. Same as in fig. 3 immediately after release from the glass tubing.

Fig. 5. Same petiole two days later.



PODOPHYLLUM PELTATUM



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INDEX TO AMERICAN BOTANICAL LITERATURE
1921–1927

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CORRECTIONS

for Bull. Torrey Bot. Club, vol. 54, no. 3, March, 1927

For "*Lamprothamnus alopercoides*" read "*Lamprothamnus alopecuroides*" on pages 188, 192, 195, 213, 216, 217, 227, and 229.

For "Henry Allen Gleason" read "Henry Allan Gleason" on front page of cover.

On page 233 add "Leaves serrate or dentate never creno-serrate; summer shoots glabrous or tomentose" as the second main lead of the key, aligning this on the left with "Leaves creno-serrate; summer shoots tomentose."

On page 247 add foot-note "[6]Ashe, Bull. Charleston, S. Car., Mus. 32. 1925."